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A TEXTBOOK  
OF  
GENERAL BOTANY

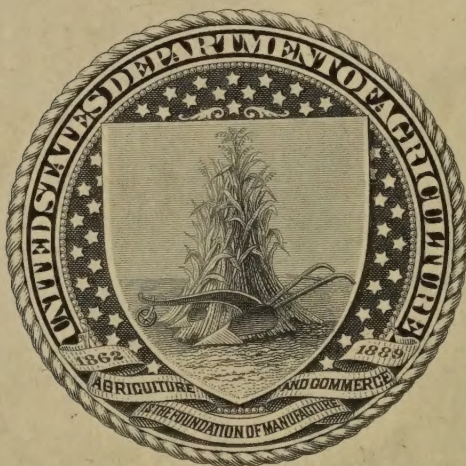


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# A TEXTBOOK OF GENERAL BOTANY

BY

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## PREFACE

In this book an attempt has been made to treat botany from the standpoint of general principles rather than as illustrated by special plants used as types, and from a world point of view rather than from a local one. This method is more likely to give the student a broad outlook, and makes the book suitable for any climate or region. The writer has had teaching experience in both temperate and tropical regions, and believes this method preferable for students in either region, not only because it gives them a broad outlook but also because it avoids many misconceptions.

There is probably greater similarity in the botanical features of tropical and temperate regions than is generally realized. The writer has failed to find any set of facts which should be taught to students in the one region and not in the other. The vegetation of the temperate zone is, in general, more specialized than that of the tropics, but the features which in temperate countries are the result of cold are paralleled in the tropics by similar features which are connected with a dry season. Bizarre plants are rare in any cultivated region, and such curiosities as *Rafflesia* and *Nepenthes* are less familiar to the average tropical student than is *Dionaea* to the average American.

Treating principles rather than individual species leads the student to realize that he is studying plants in general rather than a few selected kinds, and this realization greatly enhances the value of the knowledge obtained. In this book the names of the species used to illustrate structures are given in the legends to the illustrations rather than in the text, and in many cases these names might just as well have been omitted. This method of handling the illustrative material tends to make the book general rather than provincial.



Other features which give the book a universal aspect consist in methods of presentation rather than in selection of subject matter, except in so far as widely known species are used in the illustrations. Good examples are afforded by such subjects as deciduous leaves, annual rings, and rings of bud-scale scars. In temperate countries these are associated with a winter season, but they are also found in many tropical trees that are native to regions with a seasonal climate, and in this case they are connected with a dry season. Obviously such features should be considered in any general text, but they should be treated in relation to adverse conditions rather than as universal phenomena. This will emphasize their meaning to the student, and at the same time will let him know that they are not characteristic of all trees.

The greater part of the book is devoted to the morphology, physiology, and reproduction of the seed plants, as these plants are of the greatest interest to the student on account of their importance in his environment. The plant is treated as a working machine, physiology and morphology being taught together, as in this manner both are most interesting and most easily understood.

The writer has given this course to seventeen classes, and mimeographed editions have also been used in the University of the Philippines by Professors Kienholz, Marañon, Merrill, Santos, and Shaw of the College of Liberal Arts and by Professors McWhorter and Quisumbing of the College of Agriculture, and by Professor Gutierrez in the National University. The experiences of the writer and the suggestions and criticisms of those who have used the text have been embodied in the successive editions. Great care has been taken to arrange the topics in such sequence that the student will be prepared to understand every subject when it is presented, and that the necessity of advanced or deferred explanations will be obviated. Only such subjects as the student may be expected to master and remember are included. Nothing is simply mentioned, as mere mention without information sufficient for an understanding is more likely to confuse than to instruct.



The proportion of space devoted to the lower plants is less than in many texts, and can easily be still further reduced by omitting some of the forms, which are treated separately except in the paragraphs on relationship. The writer has always omitted a number of forms when giving the course in a half year.

The illustrations were made for this book, under the direction of the writer, with the aim of having them well drawn and accurate. Good drawings not only are best for purposes of instruction but are an inspiration to the student and an incentive for him to make good ones himself. The student can hardly be expected to make good drawings if those in his text are poor.

THE AUTHOR .



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# A TEXTBOOK OF GENERAL BOTANY

## CHAPTER I

### INTRODUCTION

**Definition.** Botany is the science that deals with plants, and in its broadest sense may be said to include all the systematized knowledge of plants. As a more or less systematized science botany began with Aristotle (384–322 B.C.). Since his time knowledge of the subject has increased tremendously, and the field it now covers is so extensive that no one man could possibly be more than very superficially acquainted with all of its branches. As a result this science has been divided into a number of subordinate sciences, such as *systematic botany*, the classification of plants according to their relationships; *morphology*, the structure of the different parts of plants; *physiology*, the functions of plant organs; *plant geography*, the distribution of plants; *genetics*, which deals with inheritance and variation; and *applied botany*, which embraces *agriculture*, *horticulture*, *forestry*, *pharmacognosy*, *bacteriology*, *plant pathology*, etc.

**Value of botanical study.** The study of botany is useful for its practical applications as well as for its general educational value.

Plants are probably the most conspicuous elements in the natural environment of most people, and it is through plants that a large part of the human race comes most frequently in contact with nature.

The food of all animals, including man, comes from plants, either directly or, indirectly, through other animals. Plants furnish us much of the material from which our clothes are made. They also supply us with the wood that we use for fuel, for making furniture, for building houses, and for many other purposes. They furnish us with numberless valuable products,

such as many kinds of medicine, perfumes, paper, etc. In breathing, animals take in oxygen. This is combined with carbon, forming carbon dioxide, which is exhaled. All of the available oxygen would soon be exhausted and all animals exterminated if it were not for the fact that plants take in carbon dioxide, utilize the carbon, and liberate the oxygen.

Even the remains of plants that have long been dead are useful to man. Among these are coal, which is used for fuel and which also yields gas, coke, and coal tar. The last named is the basis of the synthetic-dye industry and the source of many valuable medicines and other useful products.

As human life is so intimately connected with and dependent upon plants, it is only natural that botany should be a subject of great interest; and it would seem that all educated persons should have some knowledge of it, if only for the purpose of understanding better so important a part of their environment as the vegetable kingdom. Such knowledge can hardly fail to give one a keener appreciation and enjoyment of nature.

While botany has great cultural value, the science is even more important on account of its useful applications. The applied branches, which are sometimes known as economic botany, are the most practical parts of the subject, but the theoretical branches also are useful. Although some of the applied branches, such as agriculture, horticulture, and forestry, have long since been separated from the parent science, their scientific application is dependent upon a knowledge of the fundamental principles of botany, and these applied branches have been continually improved by the employment of new principles discovered in the more theoretical fields. A knowledge of botany is useful not only to those engaged in the applied branches but also to everyone in daily life. It teaches us the values of different kinds of food and enables us to understand and control such processes as the spoiling of food, the decay of wood, the contamination of water supplies, and the molding of leather. Many uses will be evident as the student acquires familiarity with the subject.

## CHAPTER II

### THE PLANT AND ITS ENVIRONMENT

**The plant.** All living organisms are grouped into two kingdoms, the animal kingdom and the plant kingdom. The members of these two kingdoms are very similar in their fundamental constitution and vital processes. Plants, like animals, are living and breathing organisms characterized by growth and reproduction.

Like animals, plants range in size from very large species to minute ones that can be seen only with the aid of a microscope. In dealing with the larger and more conspicuous kinds it is very easy to tell whether a given organism is an animal or a plant. This, however, is not the case with all small species, and there are whole groups of organisms which have been regarded by zoölogists as animals and by botanists

as plants. It would, therefore, be difficult to give a definition that would include all plants and exclude all animals. As the larger and more complex plants are the ones that are most



FIG. 1. An eggplant with roots, stem, leaves, flowers, and fruit. (Plant  $\times \frac{1}{4}$ , single flower  $\times \frac{3}{4}$ )



important and most conspicuous, we may for the present confine ourselves to a discussion of these. The typical higher plant is an organism with fruits, flowers, leaves, one or more stems,



FIG. 2. A tropical orchid (*Dendrobium anosmum*), attached by means of its roots to the trunk of a tree.

( $\times \frac{1}{8}$ )

and roots. Fig. 1 represents these various parts in the case of an eggplant.

**Leaves.** The green color, which is due to the presence of a green coloring matter called *chlorophyll*, is one of the most important characteristics of the typical higher plant. Chlorophyll, in the presence of sunlight, enables the plant to manufacture sugar from carbon dioxide (a gas found in the air) and water (obtained from the soil). The sugar is the starting point from which all the complex chemical compounds found in the plant are built. The roots of the plant take from the soil not only water but, in addition, simple chemical compounds which are also used in the elaboration of the more complex and important plant materials. The manufacture of sugar from carbon dioxide and water is the chief function of the leaves of a plant. This process is known as *photosynthesis*.

Animals do not possess chlorophyll and are unable to build up their food substances from carbon dioxide, water, and simple mineral salts, but are dependent upon plants for food which has already been elaborated. Plants can and usually do remain in one place, where they absorb all the substances which they



require. Animals, on the other hand, must either move about in search of food or have it brought to them, as is the case with many marine animals whose food comes to them in the water. This difference in the method of obtaining food appears to be responsible for many of the distinctions between the more complex plants and animals.

**Roots.** The roots of most plants are in the ground, although there are many plants, particularly in the tropics, which grow on other plants or on rocks and have their roots in the air (Fig. 2). The chief functions of the roots are to absorb water and mineral matter and to hold or anchor the plant in place.

**Stems.** The stem serves as a support for the leaves, flowers, and fruits; for the transport of water and mineral matter from the roots to the leaves and other organs; and for conducting manufactured food from the leaves to other parts of the plant.

**Flowers.** In the flowers, male and female elements unite in sexual reproduction, a process which is very similar in both plants and animals. This process in plants is dependent on the transfer of small yellow grains called *pollen*, from sacs known as *anthers*, to the *pistils*, which contain the female elements known as *eggs*. The pollen is in many cases transferred by wind, or by insects which are attracted by the color or odor of the flowers.

The various parts of the flower of an eggplant are shown in Fig. 3. In the drawing the flower is represented as split down one side to show the different organs. The conspicuous expanded part is the *corolla*. In the center is the *pistil*, composed of a basal portion, the *ovary*; a terminal portion, the *stigma*;

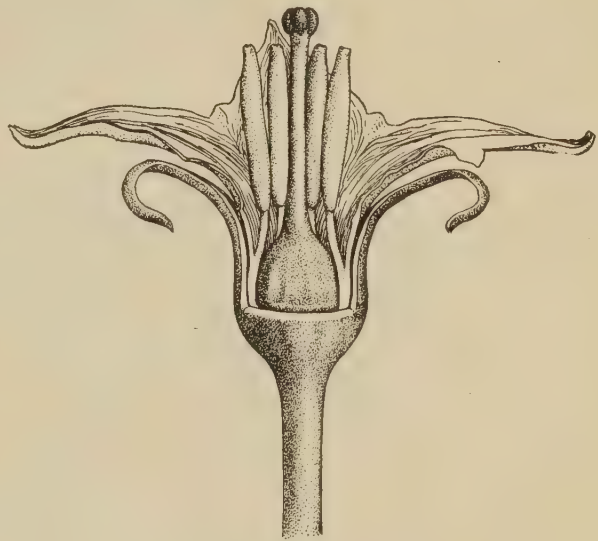


FIG. 3. A flower of an eggplant, split to show parts. ( $\times 1\frac{1}{2}$ )

and a slender structure, the *style*, which connects the ovary and the stigma. Around the pistil are the *stamens*, which consist of slender *filaments* and large terminal *anthers*. Below the corolla is the *calyx* with pointed green lobes. The calyx inclosed the remainder of the flower when it was a bud.

The process by which the male element is carried to the egg is shown diagrammatically in Fig. 4. In this figure are seen four anthers, three of which have opened so that the pollen grains are visible. When the pollen grains are deposited on the



FIG. 4. Diagram of a section of a flower at the time of fertilization

stigma, they produce long tubes which grow down into the ovary and enter small oval bodies, the *ovules*, each of which contains an egg. In Fig. 4 the pistil is represented as cut in half longitudinally. In the cavity in the ovary are shown six ovules. There are four *pollen tubes* in the pistil. The longest of these is seen entering an ovule.

**Fruits.** The male element escapes from the end of the pollen tube and fuses with the egg, after which the product of this fusion develops and becomes an *embryo*, the ovule being transformed into a *seed*. The seeds are inclosed in the *fruit*, which is the ripened ovary. When the seed meets with conditions favorable for development, the embryo grows and becomes an independent plant. The fruit not only contains the seeds but frequently serves as a means of distributing them to distant places where they may find favorable conditions for development. Examples are seen when a bird eats a fleshy fruit and later deposits the seeds at a considerable distance, or when the husk of the coconut (Fig. 304) enables the seed to float to a new locality.

All parts of the plant have separate functions, but all contribute to what, after all, is the main function of the plant, the



production of offspring. The success of the plant, if we look at it from the standpoint of the plant itself, depends not on its size or beauty but on its power to reproduce its kind and occupy territory. The leaves contribute toward this end by manufacturing food used in the seed; the stems, by giving support to the leaves and reproductive structures; the roots, by absorbing water and mineral matter and anchoring the plant in place; and the flowers, by producing the seed.

**Environment.** We have seen that a typical higher plant is an organism with leaves, stems, flowers, and fruits, all of which are in the air, and roots, which usually grow in the soil. In discussing the environment of a plant we have, therefore, to consider the component parts of the air and of the soil.

The air is a mixture of gases. The principal gases in this mixture are colorless, tasteless, and odorless, so that we cannot see, taste, or smell them. In still air even the sense of touch does not reveal their presence, and the space occupied by air may seem empty. That this is not the case is shown by winds, which cause us to feel the force of the movement of the gases. The phenomena of atmospheric pressure show that air has a very decided weight. The fact that air can hold up flying birds and airplanes likewise demonstrates that air is a real substance, and that the stems and leaves of plants do not grow in empty space. Not all gases resemble the principal ones in the atmosphere in being colorless, tasteless, and odorless. The gas chlorine, for example, is yellowish green, has a disagreeable taste and odor, and is very poisonous.

**Phases of matter.** In general the same substance may exist in three forms, or phases, — namely, solid, liquid, and gas, — depending on temperature and pressure. Water affords a good example of the three forms of a single substance. At temperatures above  $0^{\circ}$  C. and below  $100^{\circ}$  C. water exists as a liquid. When it is cooled below  $0^{\circ}$  C., it becomes a solid which we call ice. If it is heated to  $100^{\circ}$  C. or more, it changes into a gas known as water vapor. This gas is colorless, tasteless, and odorless, so that when it is mixed with the gases of the atmosphere

we cannot detect its presence by sight, taste, or smell. It is, however, easy to demonstrate that water exists in the air. When a vessel containing a cold liquid, such as ice water, is left in a room where the air is considerably warmer than the sides of the vessel, we find that water collects on the outside of the vessel. This is due to the fact that the low temperature of the vessel causes water vapor to condense to water.

**Gases of the atmosphere.** The principal gases of the atmosphere are nitrogen, oxygen, carbon dioxide, and water vapor. Nitrogen composes about four fifths of the air, and oxygen about one fifth. Carbon dioxide is always present in small quantities, while water vapor occurs in varying quantities, depending on the circumstances.

In respiration (breathing), plants and animals take in oxygen ; without it they could not carry on respiration and so would soon die. Respiration is performed in all the living parts of plants and is just as important for plants as for animals. We can see this readily in the case of seeds, which, if deprived of oxygen, will not germinate.

Carbon dioxide, as we have seen, is used by plants for the manufacture of sugar.

The water vapor in the air is also an important factor in the environment of plants. The principal constituent of the living parts of plants is water, and plants expose moist surfaces to the air. When water or a moist surface is exposed to the air, some of the water is changed to water vapor and mixes with the air. This process is known as evaporation. If a small amount of water is left in an uncovered glass, we know that the water evaporates and leaves the glass dry. We also see the result of evaporation when we dry wet clothes. The rate of evaporation depends in part on the amount of water vapor in the air. We are familiar with the fact that when the air is wet it takes much longer for anything to dry than it does when the air is dry. In other words, as the amount of water vapor in the air increases the rate of evaporation decreases, because moist air will take up less water than will dry air. The moist surfaces of plants, like



any other moist surfaces, lose water by evaporation. The evaporation of water from plants is known as *transpiration* and is a very important process from the standpoint of the plant, and one that we shall examine in considerable detail in a later chapter. The rate of transpiration will naturally be influenced by the amount of water vapor in the air, the rate decreasing as the quantity of water vapor in the atmosphere increases. If a plant continues to lose water faster by transpiration than it can obtain it from the soil, the plant will wilt and finally die. It is for this reason that many delicate plants cannot be grown in places where the air is very dry, as they would dry up and die from excessive loss of water. The amount of water vapor in the air is not the only factor which affects the rate of evaporation, as the rate is increased by wind, heat, and light.

**Composition of the gases.** We have considered briefly the principal gases of the air and their importance. We may now consider their composition. All the matter on the earth is composed of ninety-two elementary substances, known as elements. Common examples of elements are iron, lead, copper, sulphur, and mercury. The gases oxygen and nitrogen are elements.

Two or more elements can be united into a single substance known as a compound. If we expose iron to the action of the atmosphere, it will combine with oxygen and form iron rust. This rust is a compound, because it is composed of iron and oxygen and can be separated into these two elements. Rust has properties which are very different from those of either iron or oxygen.

Water is a compound which is composed of oxygen and another gas known as hydrogen. Hydrogen is the lightest of gases and is colorless, tasteless, and odorless. It is an inflammable gas and, owing to its tendency to combine with other elements, exists uncombined in only very small quantities. Carbon dioxide also is a compound and is formed by the union of the elements carbon and oxygen. At ordinary temperatures carbon is a solid. It is familiar as graphite and, in almost pure form, as charcoal. Soot is a very pure form of carbon.



In writing the reactions between chemicals it is customary to use abbreviations. N stands for nitrogen ; C, for carbon ; O, for oxygen ; and H, for hydrogen.

All elements are composed of very minute particles called atoms. Two or more of these unite to form other minute particles known as molecules. Molecules are much too small to be seen even with a microscope. A molecule may be composed of atoms of the same element or of different elements. A molecule of oxygen is composed of two atoms of oxygen. A molecule of water contains two atoms of hydrogen and one of oxygen. A molecule of carbon dioxide is formed by the union of one atom of carbon and two atoms of oxygen.

The formula for a molecule of oxygen is  $O_2$ . The letter O stands for oxygen, while the figure placed at the right of and below the O denotes that the molecule contains two atoms of oxygen. The formula for a molecule of water is  $H_2O$ . This formula shows that the molecule of water contains two atoms of hydrogen and one of oxygen. The formula for carbon dioxide is  $CO_2$ , which denotes that the molecule contains one atom of carbon and two of oxygen.

The elements oxygen, hydrogen, and carbon are very important constituents of plants. Hydrogen is obtained from water, oxygen from both water and the air, and carbon from the carbon dioxide in the air. The other elements needed by plants are taken from the soil.

**Soil.** The soil is composed of small rock particles mixed with varying quantities of decaying organic matter. Between the particles are spaces which usually contain air. The air in these spaces is very essential to plants, as it contains oxygen which enables the roots to carry on respiration.

The soil particles are surrounded by thin films of water. The roots of plants absorb water from these films. In very wet soil the spaces between the soil particles may be filled with water. This is a very bad condition for most crops, as the water keeps the air out of the spaces and the soil then contains too little oxygen for the roots of most plants.

The soil particles are composed of a number of different compounds. Small quantities of these go into solution in the water around the particles and pass into the roots of plants. The elements which are necessary for plants and which are obtained from the soil are nitrogen, phosphorus, sulphur, calcium, iron, potassium, and magnesium.

**Habit and habitat.** There are many different environments in which plants grow, and in each case the plants are fitted by their structure for their particular environment. The kind of environment in which a plant grows naturally is known as its habitat, while the form of the plant is spoken of as its habit.

**Terrestrial, aquatic, and epiphytic plants.** Plants that grow in the ground, as is the case with most of the higher plants, are *terrestrial* plants. Those that have their habitat in water are known as *aquatic*



FIG. 5. A floating aquatic plant (*Pistia stratiotes*) that is found in the tropical and subtropical regions of both hemispheres. ( $\times \frac{1}{3}$ )

plants, or *aquatics* (Figs. 5, 72, 217). If they are submerged in the water, they are *submerged aquatics*. Those that grow perched on other plants but obtain no nourishment from the plants on which they grow are *epiphytic* plants, or *epiphytes* (Figs. 2, 85, 195, 490, 493, 506, 507). In cold temperate regions the epiphytes are mosses and mosslike plants and lichens. In warmer regions, particularly in the moist tropics, many flowering plants also grow as epiphytes. Some of the most beautiful of the orchids belong to this class (Fig. 2). Epiphytes are dependent for their water supply on rain and on water which condenses from the atmosphere.

**Xerophytes, mesophytes, and hydrophytes.** Plants that are fitted for growing in a dry habitat are known as *xerophytes* (Figs. 511–514). The cacti are good examples (Fig. 512). These plants have enlarged stems in which they store water for use





FIG. 6. A mesophytic tropical forest (Philippine)



FIG. 7. Flower and buds of *Rafflesia manillana*, a true parasite on the roots of a *Cissus* vine

*Rafflesia* has no regular leaves or stem, the flowers growing directly from the roots of the host. Another species of *Rafflesia*, *R. arnoldi*, has the largest known flowers, these being about a meter in diameter



when a sufficient supply is not available from the ground. Plants, such as aquatics, which can grow only under very wet conditions are *hydrophytes*. Most plants are not specialized to grow in either very dry or very wet habitats, but thrive under conditions intermediate between these two extremes (Fig. 6). Such plants are *mesophytes* and include the great majority of cultivated plants, such as beans, tomatoes, corn, squashes, etc.



FIG. 8. Two species of tropical mistletoe which are hemiparasites

Left, *Viscum orientale*, the root of which forms a single haustorium (absorbing organ). Right, *Loranthus philippensis*, the roots of which grow on the surface of the host and send many haustoria into it

**Parasites and saprophytes.** While most plants manufacture their own food, there are many which live on food that has already been elaborated. Those plants that send absorbing organs into living plants from which they draw their nourishment are *parasites*. As true parasites do not contain chlorophyll with which to manufacture the food they require, they do not have the green color of chlorophyll (Figs. 7, 161, 170). Some plants, however, have absorbing organs by means of which they obtain materials from other plants, and at the same time possess chlorophyll which enables them to manufacture food. Such plants are *hemiparasites*, of which the mistletoe is a good example (Fig. 8).

Another class of plants, instead of manufacturing their food, absorb it from decaying organic matter. These are *saprophytes*.



FIG. 9. *Monotropa* (Indian pipe), a saprophyte with colorless leaves. ( $\times \frac{2}{3}$ )

Numerous saprophytic flowering plants obtain their food from decomposing organic matter in the soil (Fig. 9). These, like the parasites, lack chlorophyll and are frequently colorless; they may have various colors, but they never have the green color of chlorophyll. The most numerous of the parasites and saprophytes belong to the lower groups of plants. Most of the bacteria and all of the fungi either are parasitic on plants or animals or are saprophytic.

**Annuals, biennials, and perennials.** According to the length of time they live, plants are designated as annuals, biennials, and perennials. Those that live for only one year or a single season are *annuals*; these include our cereals, such as corn, rice, and wheat, and many of our vegetables, such as tomatoes, cucumbers, etc. Plants such as beets and carrots that do not produce seed until the second summer or fall after they are planted are *biennials*. Plants like the dahlia and sweet potato that live from year to year, or through a series of years, are *perennials*.



## CHAPTER III

### THE CELL

When a portion of a plant is examined under a microscope, it is found to consist of a number of small, boxlike compartments called *cells*. A typical plant cell is shown in Fig. 10, and a section of a group of cells in Fig. 11. A

plant cell is surrounded by a firm wall called a *cell wall*, which may be regarded as a container in which the *protoplasm*, or living part of the cell, is found. Cells may be thought of as the fundamental units of all living things, whether plants or animals. The cell is the smallest unit of living matter capable of continuous independent existence and of reproduction. Very small plants or animals may consist of only a single cell, while large individuals are composed of a great many cells. An egg of either a plant or an animal consists of a single cell, which, by division

and growth, develops into a mature individual of its species. In highly developed plants and animals cells become specialized and suited to different uses. Thus, in ordinary green plants there are cells that are especially suited to the absorption of water; others, to the conduction of water; and still others, to the manufacture of sugar from carbon dioxide and water. The

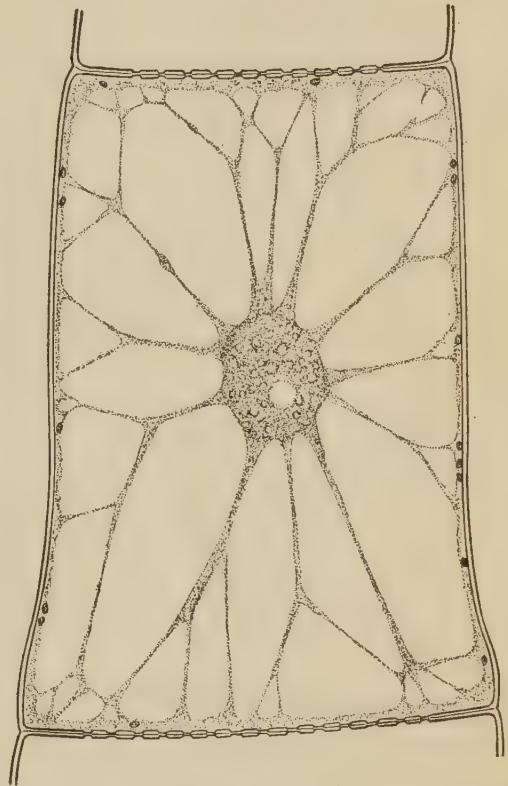


FIG. 10. A typical cell from a hair of a squash plant. ( $\times 180$ )

special characters of many different kinds of cells will be evident after a study of the different parts of a plant. All living cells are alike, however, in their fundamental characteristics.

**Cell walls.** Cell walls are important not only because they serve as containers of the protoplasm but also because they enable the plant to assume a definite shape. If it were not for the cell wall the protoplasm, being liquid or semiliquid, would simply spread out on the ground, as would any other liquid.

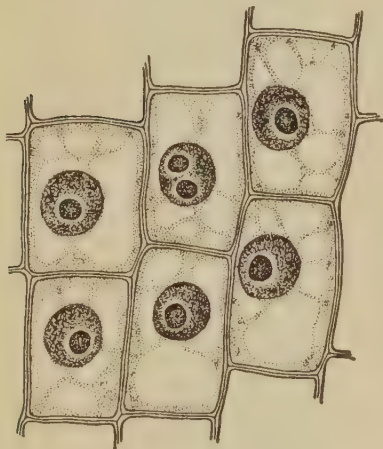


FIG. 11. A section of a group of cells from an onion root tip. ( $\times 600$ )

The heartwood of trees consists largely of thickened cell walls of dead cells (Fig. 130). If a piece of wood is examined under a microscope, the walls of the individual cells can be readily seen. The cell wall is typically composed of *cellulose*, which is a chemical compound having the formula  $(C_6H_{10}O_5)_n$  and belonging to the group of organic compounds known as carbohydrates. Cellulose is hard and colorless, absorbs water readily, and is insoluble in water. Cotton and filter paper are very good exam-

ples of nearly pure cellulose. Cellulose is well suited to the formation of cell walls, because it is rather hard and strong and because water can pass through it. Owing to its hardness and strength it gives firmness and strength to the cell wall. Since water is one of the essential constituents of plant cells, it is of great importance that the cell wall should be of some substance through which water can pass, so that water can readily enter a cell or pass from cell to cell.

Cells that are specialized for certain purposes sometimes have other substances in addition to the cellulose in the cell wall. Cell walls that are considerably thickened, so as to give great strength, frequently contain a substance known as *lignin*. Such cells are said to be *lignified*. Wood is composed largely of lignified cells. Water passes through lignin very readily, so that the addition of lignin strengthens the wall without



greatly interfering with the passage of water through it. Cells that are on the outside of plants and exposed to dry air frequently have their outside walls impregnated with a waxy substance, *cutin*. Water does not readily pass through such cell walls; consequently the walls tend to protect the cells from excessive loss of water due to evaporation. A layer of cutin is frequently found on the outside of cells that are exposed to dry air. Such a layer is known as a *cuticle*. Stems of plants are frequently protected from high rates of evaporation by the development of *cork*. The walls of cork cells also are impregnated with a waxy substance, *suberin*, which is impervious to water.

A cell can exist without a cell wall, and in some of the simpler plants, at certain times, the protoplasm escapes from the cell and surrounds itself with a new cell wall.

Animal cells do not have hard cell walls, like plants, but have a soft covering; in some cases they may be naked. For this reason the flesh of animals is soft, while the form of large animals is due to a considerable extent to their bones, and not to cell walls, as in plants.

**Protoplasm.** Within the cell wall is found the protoplasm, or living part of the cell. The gray material in Figs. 10 and 11 is protoplasm. Protoplasm is usually a viscous liquid or a jelly. There is no sharp dividing line between these two states, and the same protoplasm may change from one to the other. The liquid state is associated with a more active condition. Protoplasm has a slightly grayish color, or it may have a yellowish tinge due to included food particles. It is usually rather transparent. Included within the protoplasm are numerous minute granules, many of which are food particles.

Protoplasm is essentially a colloidal dispersion of proteins in water. Active protoplasm usually contains more than 90 per cent of water. In some cases, as in seeds, the amount of water may be much smaller, and the protoplasm becomes relatively hard. In such cases, however, the protoplasm loses most of its activity and becomes active only when additional water is

supplied. Proteins are very complex chemical compounds with large molecules and always contain the elements carbon, hydrogen, oxygen, and nitrogen, and frequently in addition other elements, such as sulphur and phosphorus. In protoplasm there are many different kinds of proteins. The white of an egg is a very good example of one kind of protein.

**Colloidal state of protoplasm.** The proteins are dispersed in the water of the protoplasm as particles of colloidal size. In order to understand what is meant by a colloidal dispersion in water (sometimes called a colloidal solution) we may consider the differences between a suspension, a colloidal dispersion, and a true solution. If we were to take small particles of soil that are still large enough to be visible, and stir them in a vessel of water, they would become suspended in the water. We should then have a suspension of soil particles in water. We frequently see such a condition in muddy rivers or in agitated pools. Each soil particle is composed of many molecules. These particles would settle to the bottom if the water were to remain still for a sufficient length of time. Each soil particle could be divided into two, and we should have a suspension of smaller particles. Theoretically this process of division could be continued until each particle would consist of only a few molecules and finally of only a single one. The last condition would be a true solution, in which the individual molecules of the soil would be dispersed in water. When we put a little sugar in water, the sugar seems to disappear and to sweeten the water. In such a case we have a solution (or dispersion of molecules) of sugar in water. From the foregoing consideration it is evident that there must be every gradation between a suspension and a true solution. The condition intermediate between a true solution (dispersion of molecules) and a suspension (dispersion of visible particles) is known as a colloidal dispersion. A colloidal dispersion in water is a dispersion of particles whose size may vary between  $0.1 \mu$  and  $0.001 \mu$ . ( $1 \mu$  equals 0.001 millimeter.) The lower limit is regarded as the size of a large molecule, while the upper limit is slightly smaller than the smallest



object of which the form can be seen with the aid of a microscope. These limits are arbitrary, as there can be no sharp division between a colloidal dispersion and a suspension. Likewise, there is no sharp distinction between a colloidal dispersion and a true solution, as some complex molecules are large enough to be within the limits of size given above for colloidal particles.

A suspension is a dispersion of particles which are large enough to be visible with the aid of a microscope. A true solution is a dispersion of molecules or parts of molecules. A colloidal dispersion is a dispersion of particles which are larger than most molecules and yet too small to be seen even with the aid of a microscope.

Colloidal dispersions are not confined to dispersions of solids in liquids. Just as we may have an emulsion (which is a suspension of a liquid in another liquid, as oil in water), so we may have a colloidal dispersion of a liquid in another liquid. This condition is known as an emulsoid. Smoke is a dispersion of a solid in a gas; a cloud is a dispersion of a liquid in a gas; meerschaum is a dispersion of a gas in a solid; ruby glass is a dispersion of a solid (gold) in a solid (glass). Proto-plasm is an emulsoid in which proteins are dispersed in water.

**Importance of colloidal state.** Much of the importance of the colloidal state arises from the fact that the dispersed substances have enormous surfaces for the play of surface forces and for chemical reactions. The increase in surface when a substance becomes finely divided can be illustrated by the following example: A cubic centimeter of material in the form of a cube would have six sides, each with an area of 1 square centimeter. The cube would therefore have a surface of 6 square centimeters. If this cube were divided into two parts by a cut in a plane parallel with two sides, the surface would be increased by the area of two sides. The two parts would then have a total area of 8 square centimeters. Subdividing these parts would, of course, increase the surface area. If the original cube were divided into cubes with edges 1 millimeter long, there would be one thousand cubes and they would have a total area of 60 square centimeters.

If it were divided into cubes with sides  $1 \mu$  (0.001 millimeter) long, there would be a total area of 6 square meters, while if the original cube were divided into cubes with edges  $0.001 \mu$  long, the total surface would be 6000 square meters.

**Hydration of protoplasm.** The particles of many colloids have the property of absorbing and holding large quantities of water. This property is known as hydration, and a colloid which has absorbed water is said to be hydrated. Gelatin is a colloid and affords a good example. A 2 per cent solution of gelatin is a solid at ordinary temperature. Thus, two parts of gelatin can hold ninety-eight parts of water. The colloids of protoplasm are hydrated, the degree of hydration varying under different conditions.

**Distribution of protoplasm.** The protoplasm is usually divided into two parts: the nucleus, a rounded body; and the cytoplasm, which is the protoplasm outside of the nucleus. These are shown in the cells in Fig. 11. Young cells are usually filled with protoplasm. In mature cells the cytoplasm may consist of a layer around the cell walls, a layer around the nucleus, and strands radiating from around the nucleus toward the cell walls (see Figs. 10, 11); or the cytoplasm may simply occur as a layer around the cell walls and the nucleus be embedded in this layer (Fig. 13). The nucleus is generally regarded as the part of the cell which governs the activities of the other parts and determines the nature and hereditary characteristics of the plant.

**Inclusions within the protoplasm.** Protoplasm consists essentially of a colloidal dispersion of proteins in water, but many other substances may be found within the protoplasm; these include mineral salts, sugar in solution, and food particles.

**Physiological properties of protoplasm.** Protoplasm is frequently said to be distinguished from nonliving matter by the following physiological properties:

1. *Absorption and excretion.* By absorption protoplasm obtains materials necessary for its growth, and by excretion it gets rid of some substances which it does not need. The protoplasm of green plants takes in water and mineral matter from the soil,



and carbon dioxide from the air. In the process of photosynthesis, sugar is manufactured from the carbon dioxide and some of the water. This sugar may be stored in the cells or changed into some other form of stored food; or it may combine with elements from the soil and be stored as food; or it may become incorporated in the protoplasm. Substances which are very different from protoplasm are thus taken into the protoplasm and then combined and made into protoplasm.

2. *Metabolism.* The sum of the processes of chemical change, including the building up and oxidation of material within the protoplasm, is known as metabolism. One of the activities of protoplasm is the combining of sugar with elements from the soil to produce proteins which become a part of the protoplasm. This is a constructive process. Destructive processes also take place in the cells of plants as complex compounds are broken down with the liberation of energy. The protoplasm uses this energy in various activities.

3. *Growth and reproduction.* The growth of protoplasm is due to changes within the protoplasm, while the growth of non-living things, such as ordinary crystals, is accomplished by the addition of layers on the outside. Reproduction is essentially the separation and growth of small portions of protoplasm derived from one or two parent organisms. Reproduction, therefore, is a form of growth.

4. *Movement.* Protoplasm has the power of moving and is frequently in motion. This motion of the protoplasm in a cell can be easily seen with the aid of a microscope. In some cases the motion is evident as an active streaming, while in others it manifests itself by changes in the shape and position of the protoplasmic masses. Fig. 12 shows three drawings, made at fifteen-minute intervals, of the same cell. The changes in the arrangement of the protoplasm are very evident. Protoplasm not only possesses the property of moving but it may also cause the motion of whole organs or even organisms. This kind of movement is more evident in the case of animals than in plants, but is easily recognized in the case of sensitive plants and in

leaves which fold together at night. We know also that the younger parts of many plants bend toward the light. Numerous small plants which live in water have the power of moving from place to place, just as is the case with animals.

5. *Irritability.* The property of responding to external stimuli is known as irritability. A good example is afforded by the effect of various stimuli, such as heat or chemicals, on the movement of protoplasm. Moderate heat increases the rate, while low

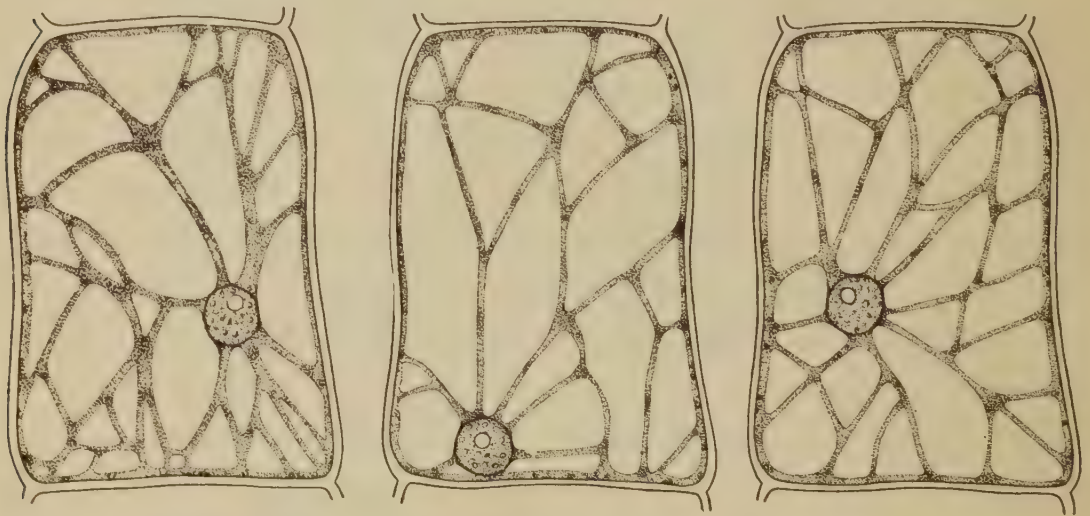


FIG. 12. Drawings, made at fifteen-minute intervals, of a cell from a hair of a squash plant

Note the changes in the arrangement of the protoplasm. ( $\times 180$ )

temperatures decrease it. Some chemicals accelerate it, while others have the opposite effect. The effect of a stimulus on protoplasm may be evident in the movement of a whole organ, as when the leaves of a sensitive plant close as the result of contact or of heat, or when a stem or a leaf bends toward the light.

**Vacuoles.** The larger part of the space within a mature cell is usually occupied by a vacuole. This is a clear space which contains water with small quantities of material dissolved in it. The principal use of vacuoles is, by enlarging the cell, to increase its absorbing surface; besides this, water, food, or waste material can be stored in them. Vacuoles are not present in very young cells, but as the cell increases in size small vacuoles appear and then gradually enlarge. As they increase in size they coalesce



to form a single large vacuole, the volume of which is usually greater than that of the protoplasm. In a large cell the protoplasm occurs as a layer lining the cell wall, while in addition there

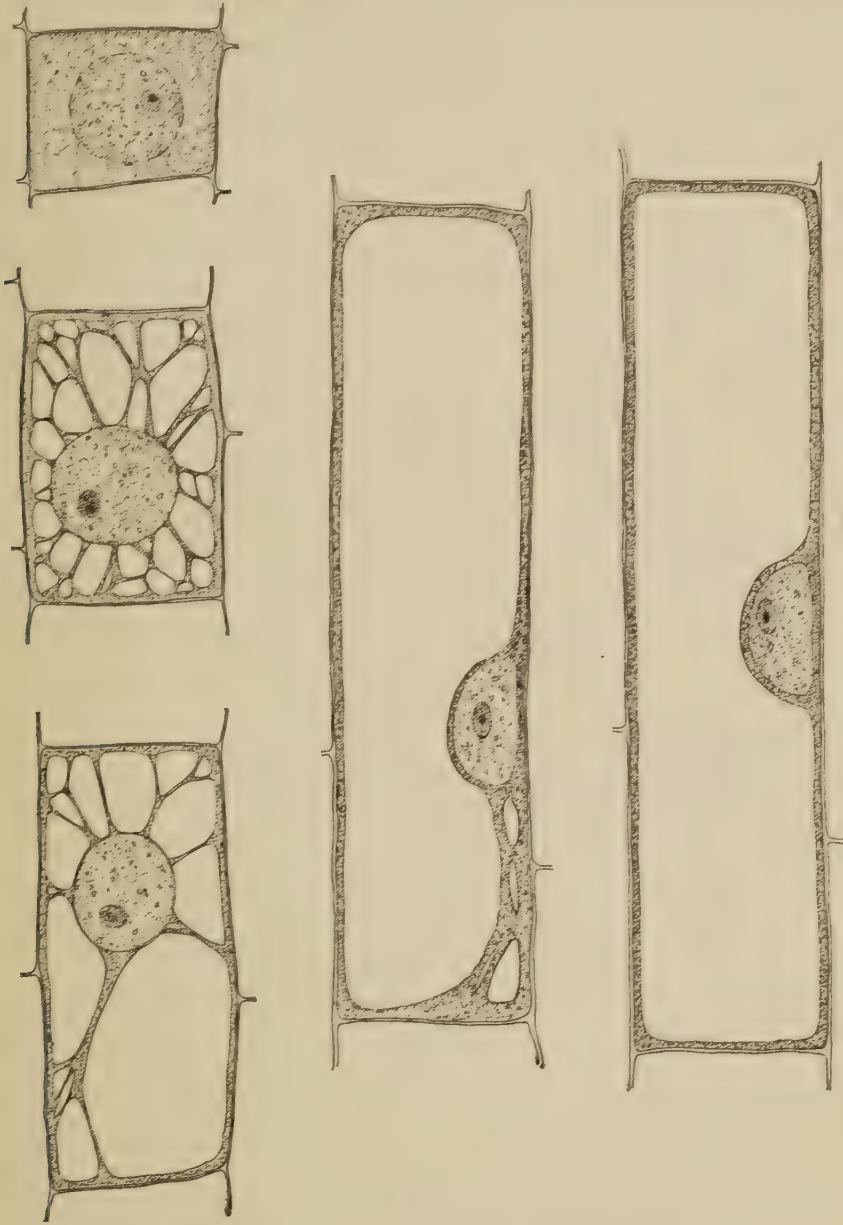


FIG. 13. Cells from an onion root

The cell in the upper left-hand corner is a young one without vacuoles, while the others show various stages in the formation and enlargement of the vacuole. ( $\times 800$ )

may be strands stretching across the vacuole. Fig. 13 shows a young cell without vacuoles, and stages in the formation and growth of the vacuole.

**Plastids.** These are definitely shaped protein bodies embedded in the cytoplasm. There are several kinds of plastids, and they have different functions. *Chloroplastids* are green bodies which are colored by chlorophyll. In the presence of sunlight, carbon dioxide and water are changed into sugar in the chloroplastids. *Amyloplastids* are white plastids in which starch is stored. *Chromoplastids* are variously colored plastids which in some

cases are responsible for the color of flowers, fruits, and other organs.

**The units of living matter.** The cell is the smallest unit of living matter capable of continued independent life and growth, but examination of a cell has shown that it is composed of a number of different smaller units, all of which combine to carry on the varied activities of the cell. In later chapters we shall have occasion to study the structure of the small units which we have observed in the cell, and we shall find that some of

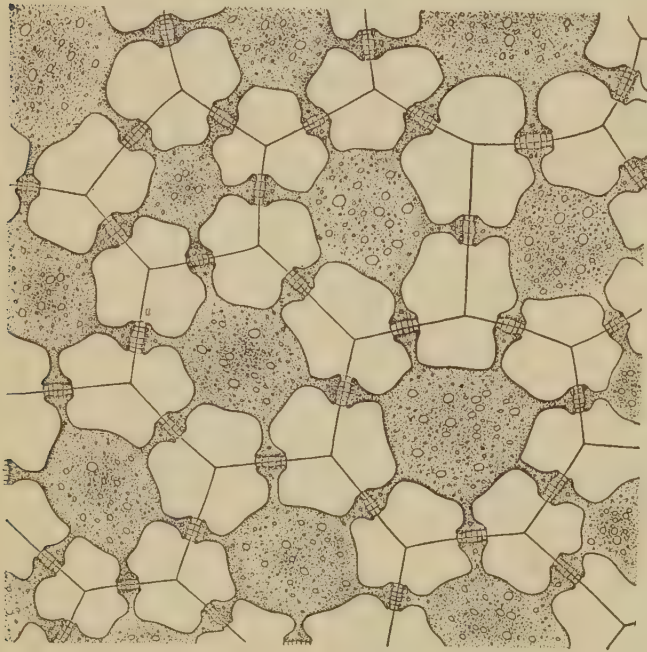


FIG. 14. Cells from the kernel of a fruit of a nipa palm (*Nipa fruticans*), showing protoplasmic connections between adjacent cells

The white areas represent thick cell walls

them are in turn very complex and composed of different kinds of smaller units. While the cell is, therefore, the smallest unit of living matter capable of continued independent existence, it is itself a very complex structure composed of many varied smaller units.

In at least many cases the cells of higher plants are not absolutely independent, as the protoplasm of neighboring cells is connected by means of fine protoplasmic strands which run through perforations in the cell walls. When the walls are thin



it is rather difficult to demonstrate these connections, but they are much more easily seen when the walls are thick. Such connecting strands are shown in Figs. 14 and 294.

**Middle lamella.** Between two adjacent cell walls there is a thin layer known as the middle lamella, which cements together the two cell walls.

## CHAPTER IV

### THE LEAF

A *leaf* is a lateral outgrowth from a stem and is, typically, a thin, expanded structure with, usually, a green color (Fig. 15).

While a number of important physiological processes take place in leaves, their principal function, and the one for which



FIG. 15. Young leaves of mulberry  
(*Morus alba*)

Stipules occur at the bases of all except the oldest; here there is a scar showing where the stipule was located. ( $\times \frac{1}{3}$ )

their structure is especially suited, is *photosynthesis*. This is the production of sugar from carbon dioxide and water in the presence of sunlight. This process takes place only where there is *chlorophyll*, which occurs in the *chloroplastids*. The sugar formed in photosynthesis is the basis from which all the complex compounds found in plants are produced. The thin, expanded form of leaves is especially suited for photosynthesis, as light, which is necessary for this process,

penetrates only a short distance into a plant. An increase in the thickness of leaves would require additional plant material without producing a corresponding increase in the rate of photosynthesis.

**Structure of leaves.** Leaves (Fig. 15) are typically composed of a broad, expanded portion, the *blade*, which is the essential part; a stalk, called the *petiole*, which is sometimes lacking; the *base*, the part which joins the leaf to the stem; and often a pair



of *stipules*, which are scalelike or, rarely, leaflike outgrowths from the base. Frequently the stipules are temporary structures and drop off as the leaf matures (Fig. 15).

Leaves are distinguished from stems by their origin, the leaf being the first lateral outgrowth from the stem (Fig. 92), while the branches grow in the axils of the leaves, that is, just above where the leaves are joined to the stem. Leaves are further distinguished from stems by the fact that the growth of a leaf is usually limited, while that of most stems is not; that is, leaves reach a certain size and then cease to grow, while stems continue to grow in length as long as the plant lives.

The blades of most leaves contain a narrow, thickened structure which is a continuation of the petiole and extends from the petiole through the center of the blade to the opposite end

(Fig. 16). This is the *midrib*. On both sides of the midrib there are lines which either are parallel with each other or form a network. These are *veins*. The midrib and veins contain conducting cells, through which water, coming from the roots, is carried to all parts of the leaf, and by means of which food, manufactured in the leaf, is conducted to the petiole on its way to other parts of the plant. The midrib and veins are also important in giving stiffness to the leaves. Some leaves do not have a single midrib but, instead, have several large veins which serve the same purpose (Figs. 54, 58).

**Venation.** The leaves of flowering plants show two very distinct types of *venation*, that is, arrangement of the veins. In one

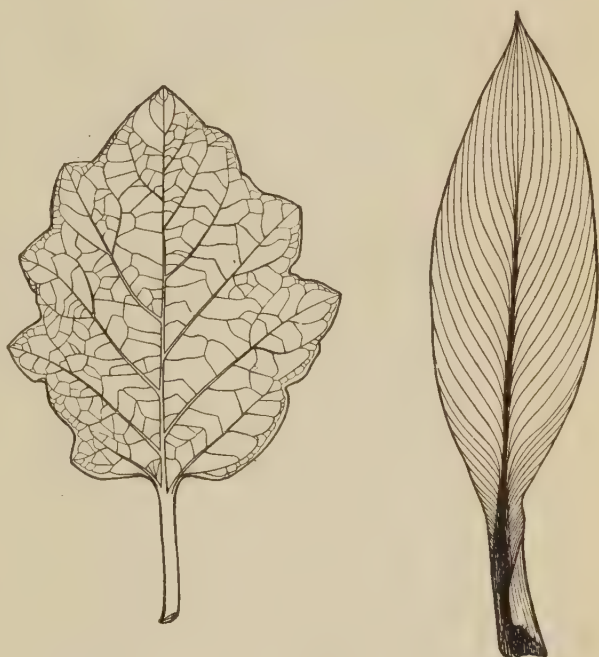


FIG. 16. Venation of leaves

Left, leaf of eggplant, showing midrib and netted veins; right, canna leaf with parallel veins

type the veins are *parallel* (Fig. 16), while in the other they form a network (Fig. 16) and are said to be *netted*. These two types of venation are characteristic of the two great divisions of flowering plants, monocotyledons and dicotyledons. *Monocotyledons* are plants with one seed leaf, while *dicotyledons* have two seed leaves. Parallel veins are characteristic of monocotyledons, and netted veins of dicotyledons, although some monocotyledonous leaves have netted veins.

### MICROSCOPIC ANATOMY OF LEAVES

**Epidermis.** The leaf is covered on both surfaces by a single layer of cells, known as the *epidermis* (Fig. 17). The outer walls of the epidermis are usually thickened and impregnated with a



FIG. 17. Cross section of a portion of the blade of a leaf (*Hibiscus*). ( $\times 285$ )

waxy substance called *cutin*.

Walls that are impregnated with cutin are said to be *cutinized*. Not only do the outer walls of the epidermis contain cutin, but their outer surfaces are frequently covered by a layer of cutin which is known as a *cuticle*. Water passes readily through cellulose, and so, if the outer walls of the epidermis were thin cellulose walls, their outer surfaces would be wet and water would evaporate from them in large quantities.

The evaporation of water from plants is called *transpiration*. As the outer walls of the epidermis are thick and waxy, water does not pass through them readily, and the transpiration of water from the surface of the epidermal cells is greatly reduced, only very small quantities



of water being lost in this manner. This restriction of transpiration is one of the most important functions of the epidermis. Another function is the prevention of the entrance of disease-producing organisms into the interior of the leaf. The epidermis also protects the soft interior from mechanical injury.

In the epidermis of the leaf are numerous small openings, the *stomata*. These are shown in Fig. 18, as seen in the surface of the epidermis. The small oval openings are the stomata, while the large, irregularly shaped cells are ordinary epidermal cells. A cross section of a stoma is shown in Fig. 17, in the lower epidermis.

Each stoma is surrounded by two kidney-shaped cells called *guard cells*. Under certain conditions these guard cells move in such a way as to open or close the stoma. The stomata allow for the exchange of oxygen and carbon dioxide between the cells in the interior of the leaf and the external atmosphere, and also permit the passage of water vapor from the interior of the leaf to the outside air.

**Distribution of stomata.** Stomata are usually found only in the lower epidermis, or much more abundantly in the lower than in the upper epidermis. This would seem to be explained in part by the fact that stomata in the lower surface are less likely to be closed by rain or by dust than are those in the upper epidermis. In leaves which float on the surface of the water stomata occur only in the upper epidermis. Submerged plants do not possess stomata.



FIG. 18. Surface view of epidermis of a dicotyledonous leaf

The oval openings are the stomata. Each is surrounded by two kidney-shaped guard cells containing chloroplasts. The large irregular cells are ordinary epidermal cells. An epidermal hair is shown at the left. ( $\times 150$ )

**Chlorenchyma.** The parts of the leaf that lie within the epidermis and between the veins are especially suited to carrying on photosynthesis. The cells in this part of the leaf contain chloroplastids and are known as *chlorenchyma* cells (Fig. 17).

**Palisade chlorenchyma.** The chlorenchyma is usually divided into two regions. The portion near the upper surface is generally composed of elongated cells which are close together, with their longest axis perpendicular to the epidermis (Figs. 17, 28, 35).

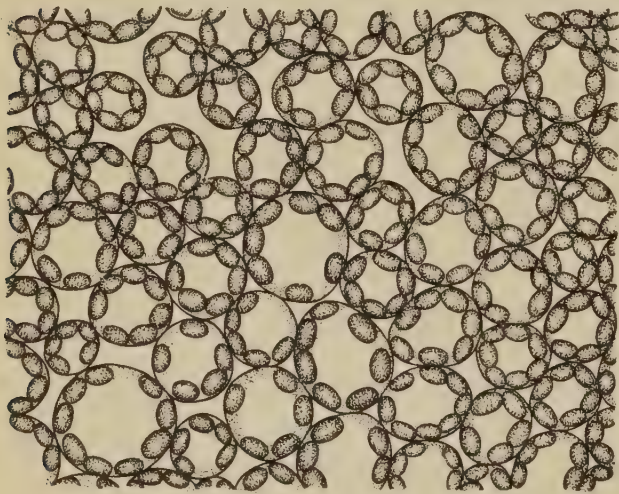


FIG. 19. Section of palisade of a leaf of Hibiscus, cut parallel with the epidermis. ( $\times 425$ )

When we look at a section of a leaf, these cells have an appearance resembling a palisade, and they are called palisade cells or *palisade chlorenchyma*. The palisade chlorenchyma may consist of a single layer of cells or of two or more layers. These cells, being near the upper surface of the leaf, are in a favorable position to receive sunlight, and their chief function is to carry on photosynthesis.

Their elongated shape is favorable to this function, as the light in going through them does not pass through many cell walls. Between the palisade cells are small air spaces which are connected with larger spaces in the lower part of the leaf, and through these with the stomata in the lower epidermis. These air spaces make it possible for gases to diffuse to and from the palisade cells. In Fig. 19 is shown a section cut across the palisade layer in a plane perpendicular to the longest axis of the cells and parallel with the epidermis. This section shows very plainly the air spaces which extend up between the palisade cells.

The cells of the chlorenchyma contain a large central vacuole and a thin layer of protoplasm lining the wall. The chloroplastids are embedded in this protoplasm and are close to the cell wall.



**Spongy chlorenchyma.** The lower portion of the chlorenchyma is known as *spongy chlorenchyma* and is usually composed of cells which are more irregular in shape and arrangement than the

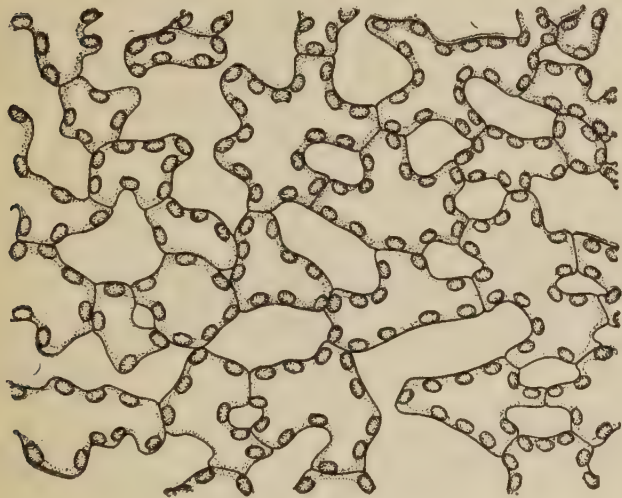


FIG. 20. Section, cut parallel with the epidermis, through the spongy parenchyma of a leaf (*Hibiscus*). ( $\times 425$ )

palisade cells (Figs. 17, 20, 28). Also, this region generally contains large air spaces. The cells of the spongy chlorenchyma contain chloroplasts and carry on photosynthesis, but they are not in as favorable a position for receiving light as are the palisade cells, and they have fewer chloroplasts. They are not, therefore, so important from the standpoint of photosynthesis as are the palisade cells. On the other hand, the large air spaces that surround these cells are near and directly connected with the stomata (Fig. 17). There is, therefore, a much freer circulation of gases around these cells than around the palisade cells, with the result that they are better suited to the exchange of gases between the cells and the surrounding atmosphere. The air spaces of the spongy chlorenchyma are not isolated chambers but a series of intercommunicating passages. While it is customary to speak of the air spaces in the spongy chlorenchyma as though there were many of them, it would be just as correct to consider many of them as forming a single large air space in which, in the case of the spongy chlorenchyma, the cells are loosely arranged. A good idea of the shape of these passages can be obtained

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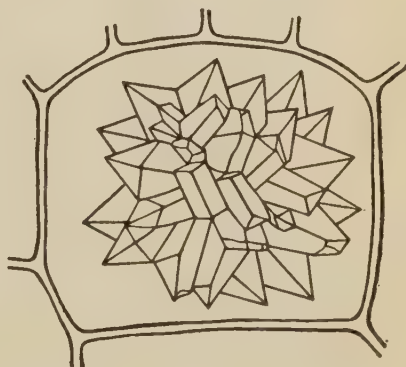


FIG. 21. Rosette crystal from cell in a leaf. ( $\times 730$ )

by comparing Fig. 17 with Fig. 20, which represents a section through the spongy parenchyma parallel with the epidermis.

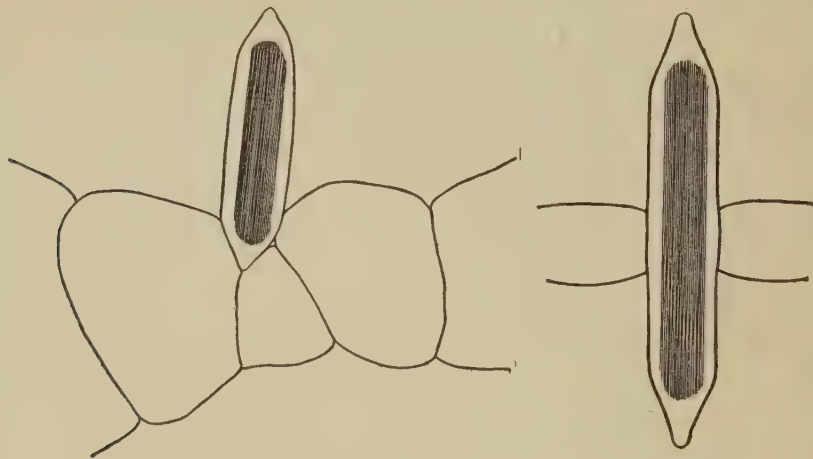


FIG. 22. Raphides from leaves

Left, taro (*Colocasia esculentum*); right, *Pistia stratiotes*. ( $\times 160$ )

Owing to the fact that the chloroplasts are closer together in the palisade chlorenchyma than in the spongy chlorenchyma, the upper surfaces of many leaves appear to be deeper green than the lower surfaces.

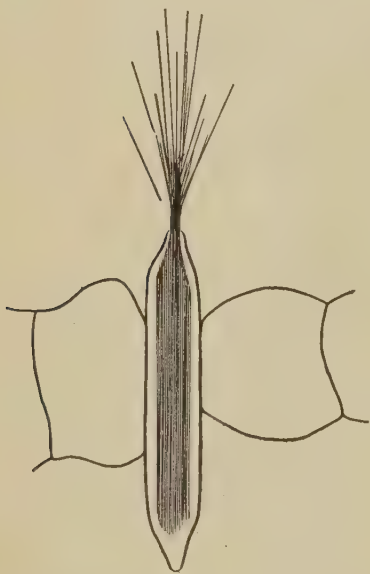


FIG. 23. Ejection of raphides from saclike cell of *Colocasia esculentum*. ( $\times 160$ )

**Calcium oxalate crystals.** The leaves and other organs of many plants contain conspicuous crystals of calcium oxalate, which appears to be a waste product. The forms of the crystals are very diverse. One of the commonest is a compound crystal having the appearance of a rosette and known as a *rosette crystal* (Fig. 21). Another common form is a long, slender crystal, or *raphide*. Such crystals usually lie parallel to each other in a bundle, which is sometimes found in a special saclike cell (Fig. 22). In certain cases these

cells have tapering end walls which are thin at the apices (Fig. 22). When the sacs are injured mechanically, the raphides are shot through the thin points (Fig. 23). Certain kinds of



raphides are very irritating and seem to afford some protection from animals, although many plants with raphides are eaten by animals. At least in some cases the pain produced is due to the entrance of an irritating substance into the wound rather than to the raphides themselves. Raphides are destroyed by boiling, and so food plants containing them are not irritating when cooked.

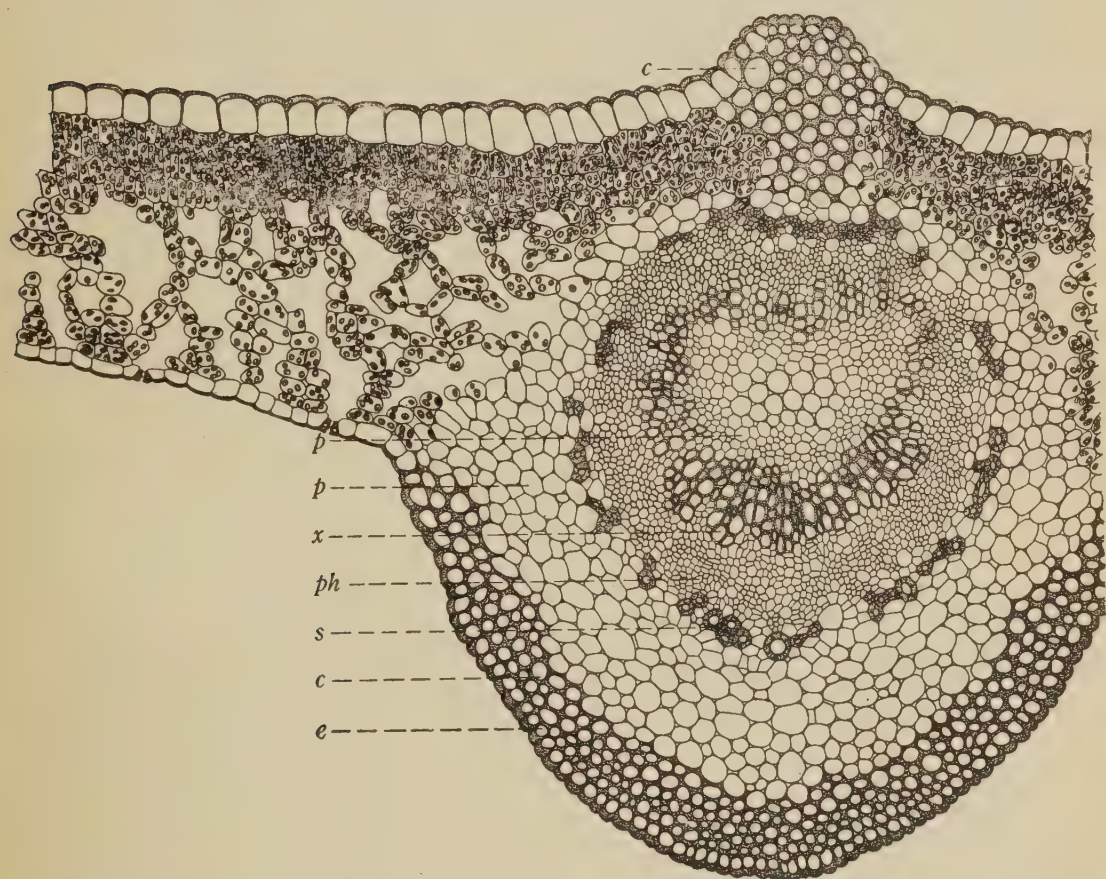


FIG. 24. Cross section of a midrib of a leaf (*Ixora*)

On the left is a portion of the thin part of the blade, showing upper and lower epidermis and chlorenchyma. *e*, epidermis; *c*, collenchyma; *p*, parenchyma; *s*, sclerenchyma; *ph*, phloëm; *x*, xylem. ( $\times 185$ )

**The midrib.** The functions of the midrib are to strengthen the leaf; to convey food, manufactured in the leaf, toward the petiole; and to carry water from the petiole to various parts of the blade. The midrib is composed of the tissues described in the following paragraphs. A *tissue* is a group of contiguous cells having the same general characteristics. Cross sections of midribs are shown in Figs. 24 and 26.

**Collenchyma.** There are two ways in which cells give strength to plant organs. In some cases the cell walls are very greatly thickened, and the thickened cell walls give strength. This is true of the wood of woody stems. Other cells become stretched by the water which is in them, and therefore are rigid. Such cells may serve to strengthen organs. Cells which are stretched by the water in them are said to be *turgid*. The rigidity derived from turgidity has some points of similarity to that of a

hose full of water, or that of an automobile tire filled with air under pressure.

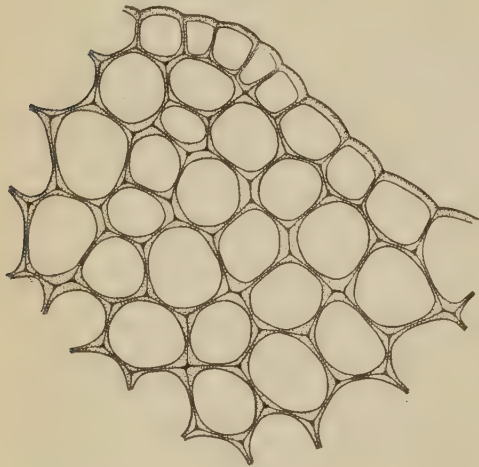


FIG. 25. Cross section through the epidermis and collenchyma of a *Coleus* stem. ( $\times 245$ )

In the center of the upper portion of the midrib, just below the epidermis, there is usually a group of cells which give strength, both by having thickened walls and by being turgid. A group of the same kind of cells usually occurs also just above the lower epidermis. These cells are known as collenchyma. In Fig. 24 the collenchyma is shown as a crescent-shaped layer

around the lower part of the midrib and just within the epidermis; also as a small group of cells extending into the projection from the upper surface of the midrib. In the section shown in Fig. 26 the collenchyma is in the same position as in Fig. 24, but is less evident because the walls are not greatly thickened. Collenchyma is composed of living cells with walls which are thickened at the angles where three or more cells come in contact with one another. This is clearly shown in Fig. 25. The thick places in the walls increase the strength of the cells, while the thin places allow for a more rapid transfer of materials from cell to cell than would take place if the cell walls were thickened throughout. These cells are more or less turgid, and so give strength to the leaf in this way also. The turgidity likewise is illustrated in Fig. 25 above.



The weight of the leaf causes it to tend to bend downward, with the result that there is a tendency for the upper portion

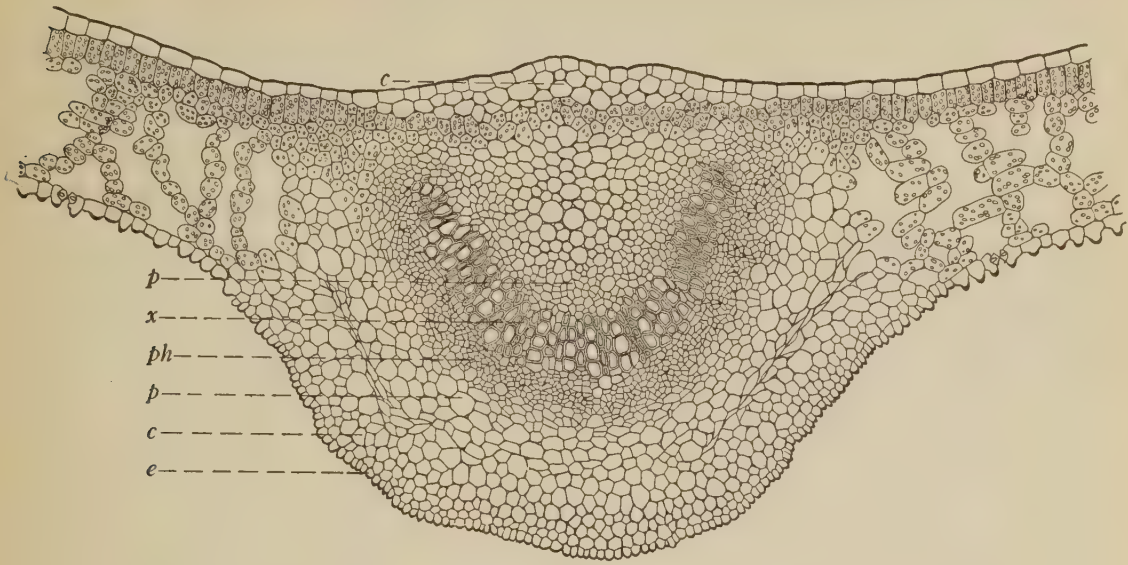


FIG. 26. Cross section of a midrib and adjoining portion of thin part of the blade of cocoa leaf (*Erythroxylon coca*)

e, epidermis; c, collenchyma; p, parenchyma; ph, phloëm; x, xylem. (× 66)

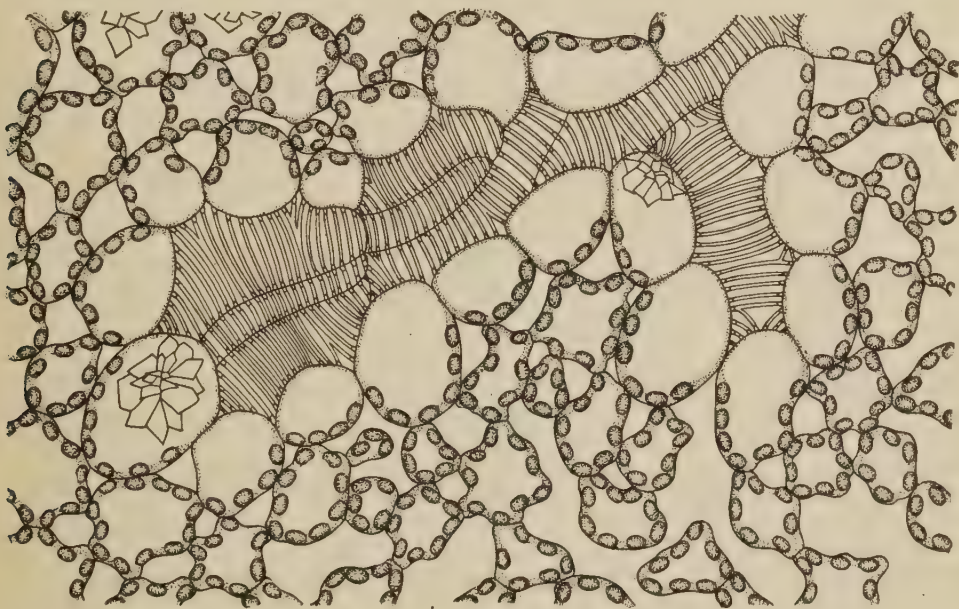


FIG. 27. Termination of veins in a leaf (*Hibiscus*), as seen in a section cut parallel with the epidermis. (× 425)

to be stretched and the lower portion compressed. The collenchyma occurs, therefore, in those parts of the midrib in which there is the greatest need for strengthening material.

**Parenchyma.** The regions between the collenchyma cells and the central portion of the midrib are occupied by *parenchyma* cells. In Fig. 24 this parenchyma is shown as a ring of tissue, which in the drawing appears to be lighter colored than any

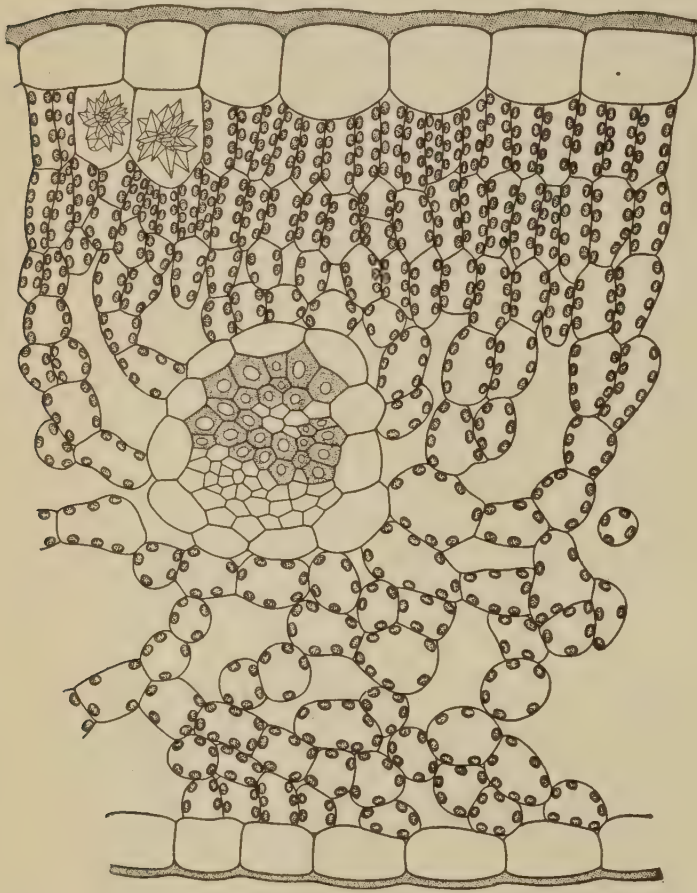


FIG. 28. Cross section of the thin part of a leaf (*Ixora*), showing the connection of the chlorenchyma with a vein

The vein is seen in the center as a compact group of cells. ( $\times 215$ )

of the tissues touching it. This lighter appearance is due to the combination of the large size of the cells, the thin walls, and the absence of chloroplasts. In structure the parenchyma cells are not specially modified for any particular function, but they perform all the general functions of cells to a limited extent. Parenchyma cells have thin walls, but on account of their turgidity they strengthen the midrib. That a considerable part of the stiffness of most leaves is due to the water in their cells can be readily demonstrated by means of leaves which have been severed from a plant. Such leaves continue to lose water by transpiration. As this water is not replaced, the cells of the leaf will contain less and less water and will lose their turgidity. We see the result when the leaf wilts and becomes soft.

**Conducting system.** The tissues composing the conducting system are situated near or at the center of the midrib. This



system, as seen in cross section, usually has the form of a ring (Fig. 24), a crescent-shaped ring, a crescent (Fig. 26), or scattered patches, but may have other shapes.



FIG. 29. Arrangement of netted veins and the free ends of the veinlets in a small portion of a leaf of a lime (*Citrus lima*). ( $\times 6$ )

If it is in the form of a ring, parenchyma cells are usually found within the ring (Fig. 24). The inner part of the ring is composed of *xylem*, which is conspicuous on account of its having thick-walled cells. Xylem conducts water and, on account of its thick-walled cells, gives strength. The conducting elements of the xylem are long tubes composed of dead cells.

The xylem ring is surrounded by a ring of *phloëm*, which is composed of thin-walled cells (Fig. 24) and serves for the transportation of food materials that come from the chlorenchyma of the leaf. When the xylem, instead of being in the form of a ring or a crescent-shaped ring, has the form of a crescent, the phloëm may occur only below the xylem (Fig. 24) or may be both above and below it.

The conducting system is better developed in the stem than in the leaf and will be considered in greater detail in the chapter dealing with the stem.

**Sclerenchyma.** Thick-walled, dead cells are frequently found scattered in the parenchyma just outside of the phloëm (Fig. 24). These are strengthening cells and are known as *sclerenchyma*. They are greatly elongated in the longitudinal direction of the

The xylem ring is surrounded by a ring of *phloëm*, which is composed of thin-walled cells (Fig. 24) and serves for the transportation of food materials that

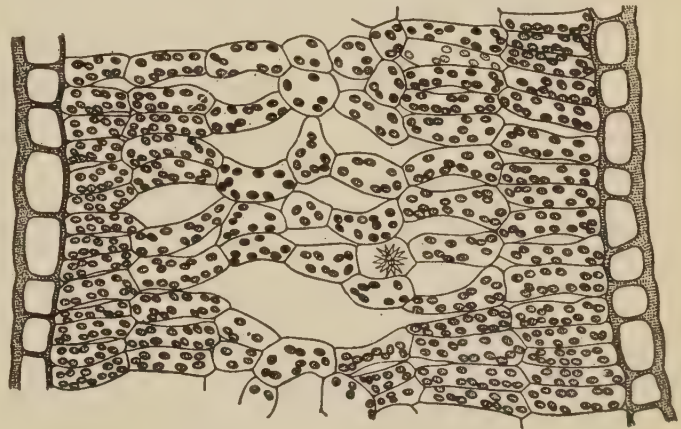


FIG. 30. Section of a vertical leaf of *Eucalyptus*, showing a palisade layer on each side. ( $\times 275$ )

midrib. Their position just exterior to the thin-walled phloëm affords mechanical protection to the latter.

**Veins.** The structure of large veins is similar to that of a midrib. The complexity of the structure decreases with the size of the veins until, near their ends, small veins consist of only one or a few conducting cells (Fig. 27). The cells of the chlorenchyma are usually arranged so that the conduction of materials to and from the veins is facilitated (Fig. 28). In Fig. 29

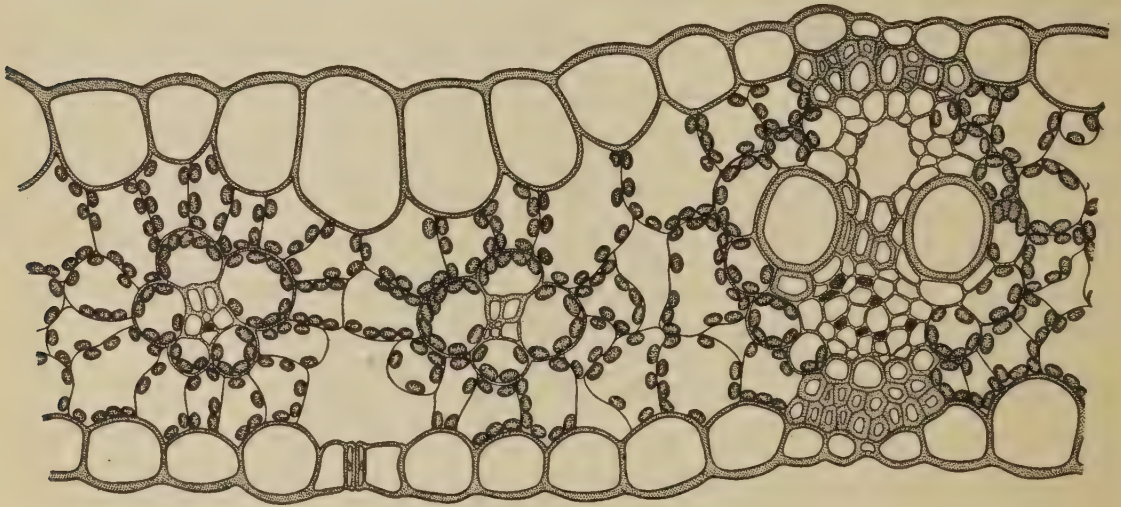


FIG. 31. Section of a leaf of Indian corn (*Zea mays*), showing the similarity in structure of the two sides of a vertical leaf. ( $\times 285$ )

are shown the arrangement of the netted veins and the free ends of the veinlets in a small portion of a dicotyledonous leaf.

**Vertical leaves.** The leaves of many species of *Eucalyptus*, instead of spreading out horizontally, hang down vertically. Both surfaces of the leaf, therefore, receive direct sunlight, and, in keeping with this fact, palisade chlorenchyma is developed on both sides, as shown in Fig. 30.

The erect leaves of grasses are very efficient and interesting types of photosynthetic organs. When grasses grow close together, the erect position of the leaves allows light to pass between them and to illuminate a large amount of surface. Moreover, both surfaces usually receive direct sunlight. The morphologically upper and lower halves therefore have similar functions, and the structure is likewise similar. In this type of



leaf the photosynthetic cells are situated around the parallel veins (Fig. 31), an arrangement which facilitates the removal of food products.

### HYDRATION

We have seen that a large part of the stiffness of leaves is due to water contained in their cells. The forces that hold water within the cell walls are not in the walls themselves but in the cell contents. The cell walls are very permeable to water; that is, water can pass through them very readily. If there were no forces in the cell contents to hold the water, the water would leak out through the walls. The term *hydration* may be used to denote the absorption and holding of water, without regard to the manner in which this is accomplished. The hydration of the cell contents is, then, the absorption and holding of water by the cell contents. This is due to two forces: the *hydration of colloids* in the cell and *osmotic pressure*.

**Hydration of colloids.** In the discussion of the colloidal nature of protoplasm, in the chapter on the cell, it was pointed out that many colloids are capable of hydration (that is, of absorbing and holding water) and that protoplasm contains hydrated colloidal particles. Protoplasm is capable of absorbing and retaining large quantities of water. When protoplasm absorbs water, it tends to swell and stretch the cell wall and thus give rigidity to the cell.

**Osmotic pressure.** When a substance is in solution, the dissolved substance tends to become equally distributed or *diffused* throughout the liquid (solvent) in which it is dissolved. This can be illustrated by the following example: If a small quantity of sugar is placed at the bottom of a vessel containing water, the sugar will go into solution and, even if there is no movement of the water, will become diffused throughout the water so that all of the water will have a sweet taste. *Diffusion* is very important in plant physiology, for by this means substances in solution in one part of a plant are frequently carried to other parts.

The force exerted by diffusion is called *osmotic pressure*. This force may be demonstrated by the use of a semipermeable membrane. A *semipermeable* membrane is a membrane through which the solvent can diffuse readily, but through which at least some of the substances which may be in solution cannot pass readily, if at all. Good examples of semipermeable membranes are animal bladders and the thin membrane around



FIG. 32. Apparatus for demonstrating osmosis

the white of an egg. When two solutions of unequal concentration are separated by a semipermeable membrane, diffusion still tends to produce an equal distribution of the dissolved substance throughout the solvent, and this results in the diffusion of the solvent from the less concentrated to the more concentrated solution. The solvent from the less concentrated solution accumulates in the more concentrated solution and dilutes it, and the tendency is for this process to continue until the two solutions have the same concentration.

The operation of a semipermeable membrane can be illustrated in the following manner: When a dilute solution of sugar in water is separated by a semipermeable membrane from a more concentrated solution of sugar in water, and the semipermeable membrane is such that water can pass through it readily while sugar cannot, the water from the dilute solution will diffuse into the concentrated solution, the tendency being for this diffusion to continue until the solutions on both sides of the membrane are of equal concentration. The operation of osmotic pressure through a semipermeable membrane may be expressed in general by saying that if two solutions are separated by a semipermeable membrane, the solvent from the less concentrated solution will tend to accumulate in the more concentrated one until the two solutions have the same molecular concentration. Diffusion through a semipermeable membrane is called *osmosis*.



The above experiment can be performed very easily with a thistle tube and a piece of parchment paper, which is a semi-permeable membrane (Fig. 32). The paper is tied tightly over the large mouth of the bulb, the tube is inverted, and the bulb is filled with a sugar solution. The tube is now set in a dish of water with the tube end uppermost and the bulb about three-fourths immersed in the water. The sugar solution will absorb water and gradually rise in the tube.

**Osmosis in plant cells.** The outer layer of the protoplasm of a plant cell is somewhat modified and is known as the *plasma membrane*. This acts as a semipermeable

membrane around the cell, while the protoplasm as a whole is a semipermeable membrane around the vacuole. These membranes are of such a nature that water passes through them readily, while some of the substances which are in solution pass less readily and some not at all. The solution in living cells is highly concentrated and is connected by means of the conducting tubes in the xylem with the roots, and through these with the water in the soil; this water is a dilute solution of mineral salts. By the forces of osmosis and hydration of colloids this water

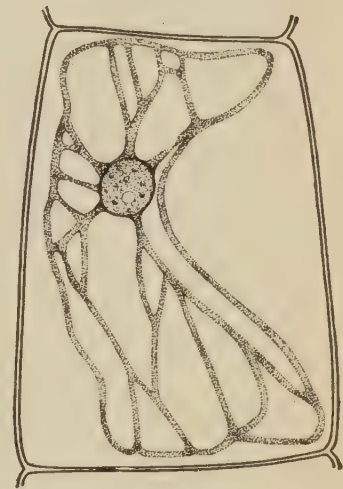


FIG. 33. A plasmolyzed cell from a hair of a squash shoot. ( $\times 160$ )

is drawn into the plant cells until the cell walls become stretched by the water. Cells that are thus stretched are said to be *turgid*, and the force of the stretching is called *turgidity*. This turgidity gives considerable strength to the cells, as explained on page 34, just as a soft hose becomes hard when filled with water, or a bicycle tire extremely rigid when filled with air under pressure.

If a cell is placed in a concentrated solution of sugar or of a mineral salt, this solution will pass through the cell wall and will draw water from the protoplasm. The removal of the water decreases the size of the cell contents so that the protoplasm is drawn away from the cell wall, as shown in Fig. 33. A cell in

this condition is said to be *plasmolyzed*. If the plasmolysis has not gone too far, the removal of the concentrated solution and its replacement by a weak solution will allow the cell contents to absorb water and resume their original distribution. When fresh-water plants or the roots of land plants are placed in salt water, they are killed by plasmolysis.

Water may pass from cell to cell by means of osmotic pressure or the hydration of colloids. When a cell which is exposed to the air is losing water, the concentration of the dissolved substances in it is increased, so that it tends to draw water from a neighboring cell. This cell in turn may draw water from another cell. In this way water may be drawn from cell to cell until the source of supply is reached.

A semipermeable membrane may be of such a nature that some dissolved substances will pass through it readily, while others will do so slowly or not at all. Some dissolved substances pass more readily than others through the semipermeable membranes of plant cells.

### PHOTOSYNTHESIS

**Definition.** Photosynthesis is the formation of sugar from carbon dioxide and water in the presence of light; it takes place only where there is chlorophyll, which is found in the chloroplastids.

**Source of materials.** The water used in photosynthesis is absorbed by the plant roots and then carried to the leaves. The carbon dioxide diffuses from the atmosphere through the stomata and then through the intercellular spaces. Carbon dioxide cannot enter the cells as a gas, but water from the cells permeates the cell walls of the chlorenchyma, and the carbon dioxide gas goes into solution in this water. As the water in the walls is continuous with that in the cells, the carbon dioxide in solution in the cell walls diffuses into the cells and finally reaches the chloroplastids.

**Process.** Photosynthesis is a very complex process concerning the details of which we have very little actual information. The first stable product seems to be some form of sugar. The various



sugars have complex molecules, however, and it would not seem probable that one of them is the first compound formed. Various intermediate compounds are postulated by different theories, but none of these theories is supported by sufficient evidence to warrant its acceptance at the present time. As the result of the photosynthetic process, *glucose* (grape sugar), which has the formula  $C_6H_{12}O_6$ , accumulates in the leaf, and this is generally regarded as the first stable product.

If we regard glucose as the end product of photosynthesis, the formula for this process may be written as follows:



This formula shows not only that glucose is formed in photosynthesis, but also that oxygen is liberated as a by-product. Moreover, the formula indicates that the number of molecules of oxygen liberated is the same as the number of molecules of carbon dioxide absorbed. This is approximately what has been observed in actual experiments.

The water and carbon dioxide that enter the reaction are very stable compounds, and the liberation of the oxygen requires energy. This energy is supplied by light, which accounts for the necessity of light for photosynthesis. Light by itself does not, however, decompose carbon dioxide or water, so that the plant must have some means of applying the energy of light for this decomposition. The application of the energy of light for the separation of oxygen from carbon dioxide and water appears to be the function of the chlorophyll.

In nature the light used in photosynthesis comes from the sun, but light from other sources can also be used.

Chlorophyll is formed in flowering plants only in the presence of sunlight. This explains why the inside of the head of a cabbage is white; it also explains the practice of banking celery in order to blanch it.

**Products.** The sugar manufactured by plants serves them as food, from which, with the addition of materials from the soil, they elaborate all the complex substances found in them.

As photosynthesis is necessary for the manufacture of all the food used by plants, it is indispensable for their existence.

Some of the oxygen liberated in photosynthesis is used by the plants in respiration, but most of it diffuses out of the cells into the intercellular spaces and then through the stomata into the external atmosphere.

When photosynthesis is active, sugar is formed much faster than it is used by the leaf or conveyed to other parts of the plant. Under these conditions much of the sugar in the leaf is transformed into *starch*, which is insoluble in water at ordinary temperatures. At night, starch is changed back into sugar and is conducted away from the leaf.

Starch and sugars belong to a class of compounds composed of carbon, hydrogen, and oxygen, and called *carbohydrates*. This name was originally given to vegetable compounds the molecules of which contain six, or a multiple of six, atoms of carbon, and in which the hydrogen and oxygen occur in the same proportion as in water. While the more important carbohydrates have these characteristics, the meaning of the term has been extended to include some related compounds which do not fit the above definition. The most important carbohydrates in plants are sugars, starch, and cellulose. Starch is one of the principal forms in which food is stored in plants. It occurs as small grains which differ in appearance according to the species (Fig. 34). Many of them show striations, owing to the deposition of successive layers.

The amount of sugar formed by photosynthesis depends upon the intensity of the light, more sugar being formed in bright than in diffused light. Many plants will not grow under the shade of others, because when in dense shade they cannot manufacture sufficient sugar to keep them alive. For this reason it is not advisable to grow crop plants too close together, as they then shade each other, with the result that the plants are not as vigorous as they should be.

On the same plant the leaves which are fully exposed to the sun are thicker than those grown in the shade. This difference in thickness is of advantage, because when the light is strong



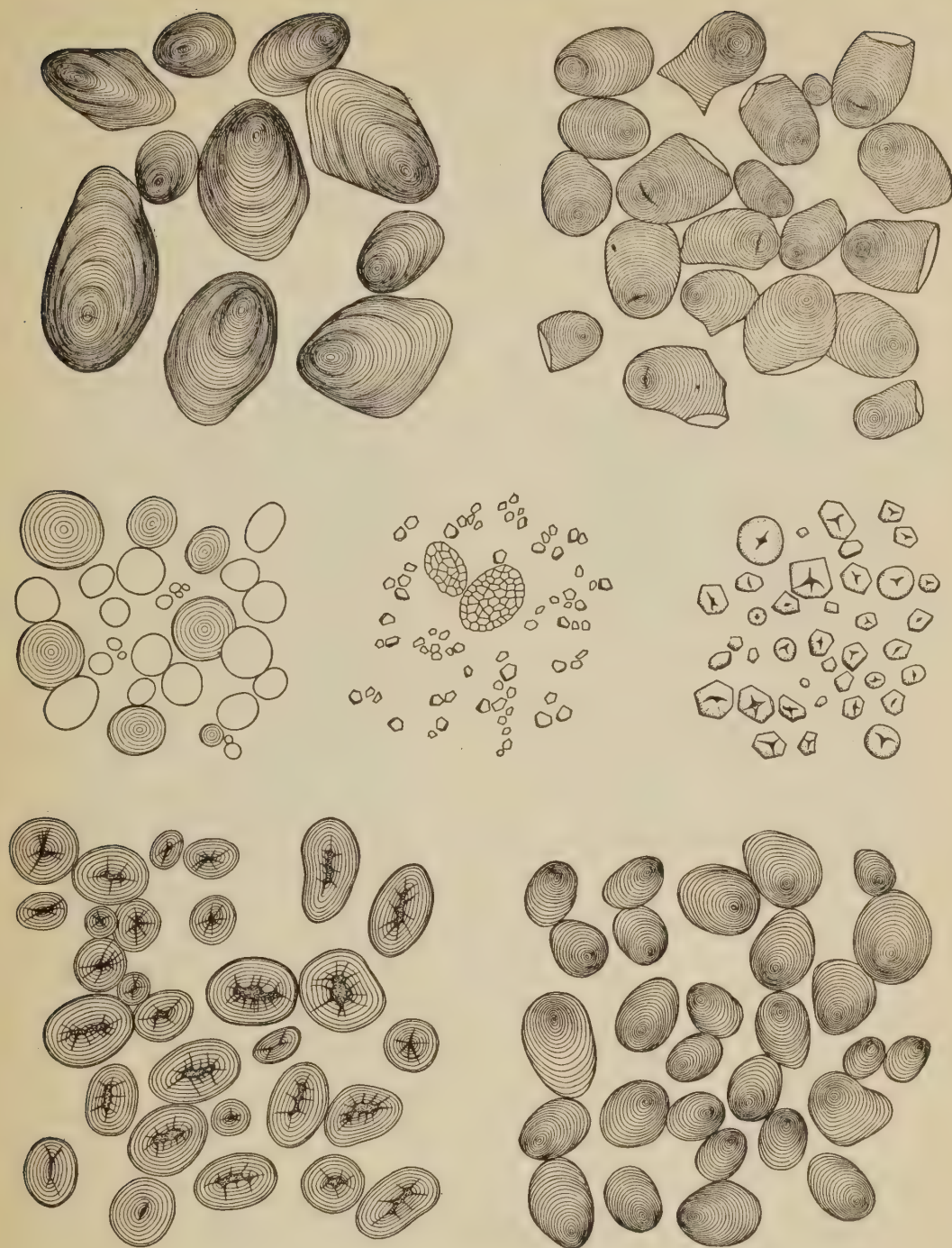


FIG. 34. Starch grains

Upper row, potato and sago ; second row, wheat, rice, and corn ; third row, bean and *Maranta*. ( $\times 290$ )

sufficient light for photosynthesis will penetrate through a thicker layer of tissue than would be the case if the light were weak. Fig. 35 shows sections of two leaves from the same plant. The one on the right was fully exposed to the sun, while the

other was more or less shaded. The leaves of many plants, if grown in different habitats, show much greater differences than those represented in this illustration.

**Demonstration.** Starch is formed in leaves very soon after photosynthesis begins. This is of great advantage in demonstrating

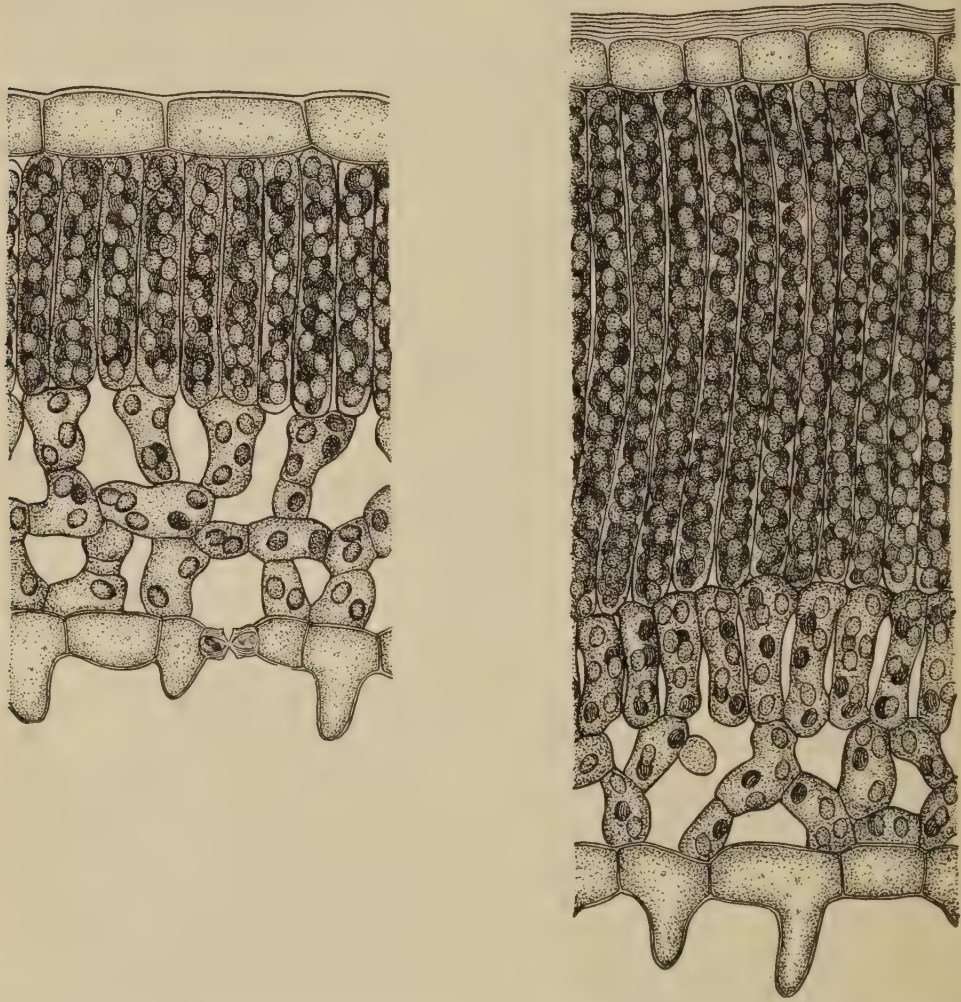


FIG. 35. Cross section of a shade leaf (left) and of a sun leaf (right) of a rain tree (*Enterolobium saman*). ( $\times 485$ )

the general facts of photosynthesis, as the test for starch is very simple. It consists in treating the material to be tested with a solution of iodine, which gives starch a blue color. In working with leaves the chlorophyll is first extracted, after which the leaves are placed in the iodine solution.

The necessity of light for photosynthesis can be shown by keeping a leaf or a part of a leaf in the dark (being careful



that all parts of the leaf have a plentiful supply of air) and then testing for starch. The leaf or the part of the leaf which was in the dark will remain white, while that which was in the light will turn blue (Fig. 36).

The necessity for chlorophyll is shown by the fact that starch is not formed in those parts of variegated leaves which lack chlorophyll.

Leaves will not produce starch in an atmosphere that lacks carbon dioxide. If a plant is placed in an atmosphere containing a known quantity of carbon dioxide, it will be found that carbon dioxide is absorbed and that the carbon appears in the leaf in the carbohydrates formed as a result of photosynthesis.

That water is used in photosynthesis is shown by the fact that the carbohydrates produced by this process contain hydrogen, which must have been derived from water.

That oxygen is given off in photosynthesis can be shown very simply by the use of certain water plants which during photosynthesis give off bubbles of gas. This can be collected by the arrangement shown in Fig. 37. If a glowing splinter is inserted into the gas, the brightness of the glow is greatly increased, thus indicating a high percentage of oxygen.

**Relation to animals.** Photosynthesis is the source of all the food of animals. Animals do not possess the power of manufacturing food from simple inorganic compounds, but must obtain food that has already been elaborated.

In respiration, animals take up oxygen and give off carbon dioxide, so that if there were no plants to separate oxygen from carbon dioxide, the supply of oxygen would be used up and animals cease to exist.

From what has been said it will be seen that, indirectly, photosynthesis furnishes man with the food he eats and the oxygen

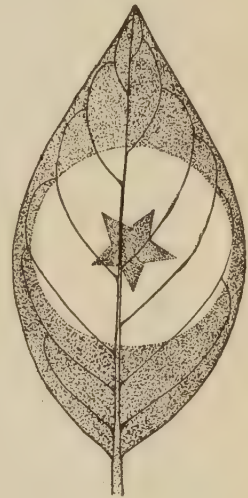


FIG. 36. A leaf tested with iodine for starch after the part showing as a star and that outside of the circle had been exposed to the light and the remainder kept in the dark

he breathes, and that it is also the source of his clothing and such of his other necessities as come from plants and animals.

**Energy.** In photosynthesis, energy derived from light is used in the liberation of oxygen. It is a fundamental principle in physics that energy is not destroyed, but that one form of energy may be changed to another, as when electricity is trans-

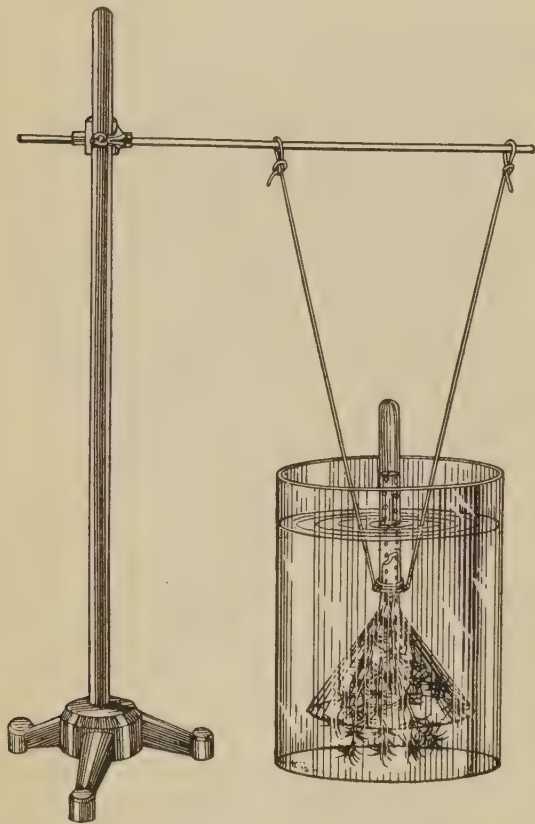


FIG. 37. Apparatus for collecting the bubbles of gas given off by a submerged plant during photosynthesis

formed into heat. The energy from the light that is used in photosynthesis is therefore not destroyed but is stored in the resulting products as potential energy. All that is necessary to release this energy is to combine the compounds resulting from photosynthesis with the amount of oxygen that was liberated in photosynthesis, and thus change them back into carbon dioxide and water. We may say, in general, that energy is used in separating oxygen from carbon or hydrogen, and liberated in combining oxygen with carbon or hydrogen. The combining of oxygen with another substance is known as *oxidation*.

When we burn wood to produce heat or light, we make use of the fact that energy is liberated in oxidation. Wood is composed largely of compounds containing carbon and hydrogen. The burning of the wood is the oxidation of these compounds, with the production of carbon dioxide and water and the liberation of energy in the form of heat and light. The energy that is released is the energy that was derived from sunlight and stored in the process of photosynthesis. Coal consists of the remains of plants, and the burning of coal releases energy



derived from sunlight and stored by plants in past geological ages. Oil is derived from plants or animals or their remains, and the energy released in the combustion of oil is also the stored energy of sunlight. We thus see that all of the energy obtained by combustion and used for industrial purposes is the energy of sunlight stored by plants in the process of photosynthesis.

Plants and animals use their food not only as building materials out of which their tissues are constructed, but also as a source of energy. This energy, like that obtained by burning wood or coal, is liberated by oxidation.

### RESPIRATION

**Definition.** The oxidation by plants or animals of compounds containing carbon and hydrogen to carbon dioxide and water, with the liberation of energy, is known as respiration.

**Importance.** The value of the process lies in the fact that it releases the energy of sunlight which was stored by the leaves in photosynthesis, so that this energy may be used for the vital activities of the plant.

All work requires energy. Moreover, the energy must be in a form suitable for the performance of the particular kind of work to be done. In the flowing of water in a large waterfall a tremendous amount of energy is expended. This energy can be used for cooking or illuminating, but in order that this may be done the form of the energy must be changed to heat or light.

In the activities of a plant, work is performed, and, like all other work, this requires energy. The green parts of plants use the energy of sunlight for photosynthesis, but energy as it occurs in light is not in a form that can be used for such vital processes as growth, movement, etc. It becomes converted into suitable form for these processes, however, when, after being stored in photosynthesis, it is released by respiration.

In this way, not only is the energy of sunlight changed to a form in which it can be used for the general vital activities of the plant, but, moreover, any excess which is stored in the

products of photosynthesis and not needed at the time may be conserved for use when it is required.

**Process.** Respiration is not a particular function of any plant organ but is carried on by all living cells. In this process, oxygen is combined with compounds containing carbon and hydrogen. This results in the breaking down of the compounds to form carbon dioxide and water, and in the liberation of energy.

If sugar is the compound that is being oxidized, we may write the formula for respiration as follows:



If we compare the above formula with that previously given for photosynthesis, we find that one is the reverse of the other, which is in keeping with the fact that photosynthesis stores energy, while respiration releases it.

**Source of oxygen.** In leaves that are carrying on photosynthesis, oxygen which is liberated by this process is used in respiration. If photosynthesis is rapid, however, more oxygen is liberated than is used in respiration, and the excess diffuses from the cells into the intercellular spaces and thence into the external atmosphere. This is the case under ordinary conditions in bright light.

Plant organs, such as petals and roots, which do not contain chlorophyll obtain oxygen from the air. The same is true of leaves when they are in the dark and so are not liberating oxygen by means of photosynthesis. In this case oxygen in the intercellular spaces goes into solution in the water held in the cell wall. It then diffuses in this water until it enters the protoplasm, where it can be used for respiration.

**Fate of products.** The water produced by respiration mixes with the water of the cell.

In the case of organs without chlorophyll or of green organs in the dark the carbon dioxide diffuses out of the cell into the surrounding atmosphere. In green tissues which are actively carrying on photosynthesis most of the carbon dioxide will be used in photosynthesis without leaving the cell in which it is produced.



From the above it will be seen that when a plant organ, from lack of chlorophyll or light, is not carrying on photosynthesis, it will, owing to respiration, absorb oxygen and give off carbon dioxide. When photosynthesis is active in green tissues, more oxygen is liberated by photosynthesis than is used in respiration, and more carbon dioxide is employed in photosynthesis than is produced by respiration, with the result that these tissues will absorb carbon dioxide and give off oxygen.

Whether leaves in light give off carbon dioxide or oxygen will naturally depend on whether more carbon dioxide is produced by respiration or is used in photosynthesis. With very feeble light the respiration of leaves may produce more carbon dioxide than is used in photosynthesis, and so the leaves absorb oxygen and give off carbon dioxide even when they are performing photosynthesis slowly. On an average day, however, the products of photosynthesis must be built up in the green tissues much more rapidly than they are broken down by respiration. A surplus must be accumulated to supply material for the respiration of the organs lacking chlorophyll, and also for the respiration of the green tissues themselves at night. In addition, building material must be produced for the growth of the plant body.

**Demonstration.** If germinating seeds are inclosed in a vessel containing ordinary air, it will be found that the oxygen is absorbed and replaced by carbon dioxide. The same phenomenon can be shown by using green plants if they are kept in the dark.

A very simple method of demonstrating the exchange of gases in respiration is that shown in Fig. 38. A few germinating seeds are placed in the bottom of a test tube and held in place by a small amount of cotton. The test tube is then inverted over a solution of potassium hydroxide. The carbon dioxide that is

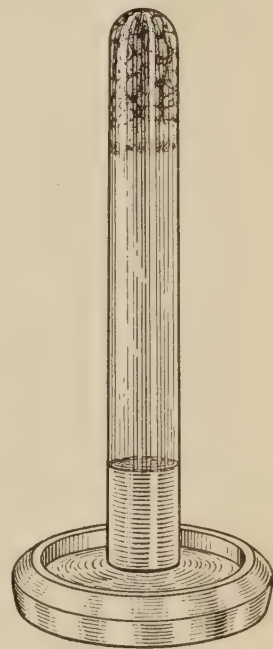


FIG. 38. Method of demonstrating respiration of seed

given off by the seeds is absorbed by the solution, so that as oxygen is taken up the solution rises in the tube. This experiment can be checked by placing germinating seeds in another tube and inverting the tube over mercury, which does not absorb carbon dioxide. The mercury will not rise in the tube, because the oxygen that is taken up by the seeds is replaced by carbon

dioxide, and, as the latter is not absorbed by the mercury, the volume of gas is not decreased. A green leaf can be used in place of the seeds in this demonstration if the preparation is kept in the dark.

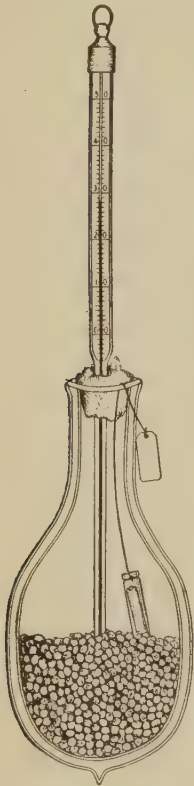


FIG. 39. Apparatus for demonstrating liberation of heat in respiration

Heat is produced by respiration. This can be demonstrated by the arrangement shown in Fig. 39. A vacuum flask is partially filled with germinating seeds. A vial containing potassium hydroxide is also placed in the flask to absorb carbon dioxide. A thermometer is then inserted through the mouth so that the bulb is among the seeds. The mouth is now plugged with cotton, which allows air to enter the flask. The heat produced by respiration causes the mercury to rise in the thermometer. This experiment should be checked by setting up a preparation similar to the one just described except that the germinating seeds are replaced by dead ones. In the latter case the thermometer will not show a rise in temperature.

**Respiration in plants and animals.** Respiration is fundamentally the same process in both plants and animals, and consists essentially in the liberation of energy by the oxidation of compounds containing carbon and hydrogen. The methods by which oxygen enters the body and carbon dioxide leaves it are very different in the higher groups of the two kingdoms. These processes, however, are only incidental to the fundamental one of oxidation. Also, the methods by which the materials to be oxidized are obtained are very different in green plants and in



animals. The plants themselves manufacture these materials, while animals must obtain them, either directly or indirectly, from plants. These processes are, however, not a part of respiration.

Respiration is equally essential in plants and animals, as it is the source of energy for vital activities. When respiration ceases, there is no further supply of energy for these activities, and death ensues.

**Oxygen supply.** Since respiration is a process of oxidation, a plentiful supply of oxygen is one of the prerequisites for normal respiration. If the supply of oxygen is inadequate, respiration will be checked, and this will limit the rate of vital activities, such as growth, which are dependent on the energy liberated by respiration.

Plants will live for a time in an atmosphere that does not contain oxygen. In this case energy is obtained by a process known as *anaërobic* or *intramolecular respiration*. In anaërobic respiration, energy is liberated by the incomplete breaking down of carbohydrates. Carbon dioxide and, usually, alcohol are produced. Anaërobic respiration is less efficient than normal respiration. Much more material is broken down, and, as a rule, much less carbon dioxide is produced.

Sufficient oxygen is available for the aërial parts of plants, but this is not always true of roots and seeds in the ground. The soil should be porous and should contain air in the spaces between the particles. If there is so much water in the soil that it interferes with the diffusion of sufficient oxygen to the roots, the growth of the latter will be retarded. For this reason soil should be well drained. The roots of plants may be killed if the ground is flooded for a considerable length of time. The same thing may result if the level of the ground around a tree is raised until the roots are buried so deeply that sufficient oxygen does not reach them. Seeds respire actively during germination, and so will not germinate without a sufficient supply of oxygen.

Plants that are partially submerged in water usually contain special aërating devices to facilitate the diffusion of oxygen from the air to their submerged organs (Figs. 197, 516, 517). The

petiole of a water lily contains conspicuous air spaces (Fig. 40), through which oxygen diffuses from the leaf blade toward the parts of the plant in the soil.

**Temperature.** Under ordinary conditions the rate of respiration increases with the temperature. The rate is very low at  $0^{\circ}\text{C}$ . and high at  $30^{\circ}\text{C}$ . This is one of the reasons why fruits

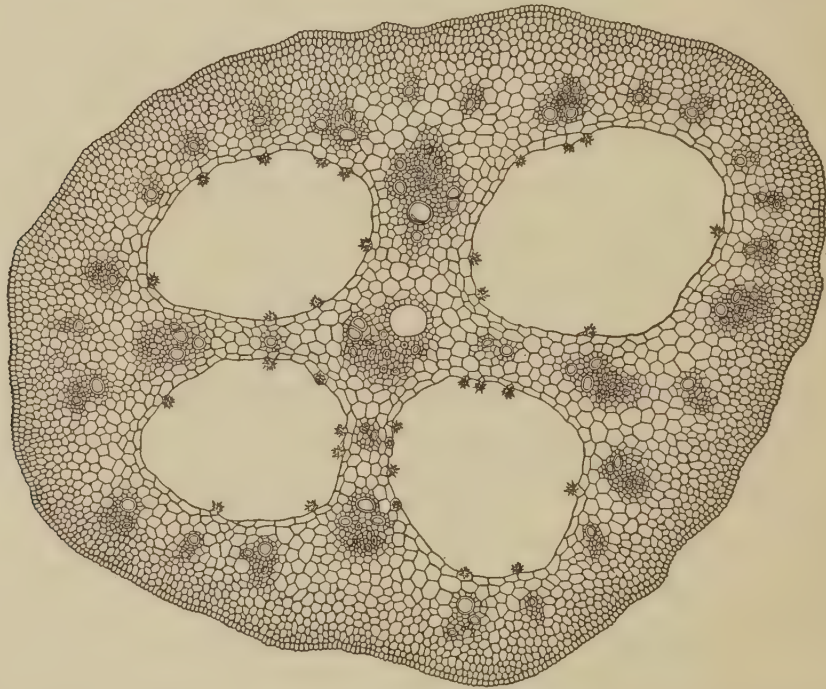


FIG. 40. Cross section of a petiole of a water lily (*Nymphaea stellata*), showing large air passages. ( $\times 30$ )

and vegetables keep better in cold storage than at high temperatures. The low temperature inhibits not only the respiration of fruits in storage but also the respiration and growth of decay-producing organisms.

### TRANSPIRATION

**Definition.** Transpiration is the evaporation of water from plants, the water passing in the form of water vapor into the surrounding atmosphere.

**Process.** We have seen that water permeates the walls of the chlorenchyma cells, so that the surfaces of the walls surrounding the intercellular spaces are wet, and that this condition is



necessary for the entrance of carbon dioxide into the cells. Since the wet surfaces of the cells are in contact with the air in the intercellular spaces, some of the water in the walls vaporizes and diffuses into this air, just as the water from wet clothes goes into the surrounding atmosphere while the clothes are drying. The accumulation of water vapor in the air in the intercellular spaces makes the water content of this air greater than that of the atmosphere surrounding the leaf, so that water vapor diffuses out through the stomata into the external atmosphere. The diffusion of water vapor from the intercellular spaces into the atmosphere tends to reduce the water content of the air in the intercellular spaces, and thus causes additional water to leave the cell walls and enter the intercellular spaces. The passage of water from the cell walls into the intercellular spaces, and then out through the stomata into the external atmosphere, is thus continuous as long as the cell walls are wet and the stomata are open. Since those conditions are necessary for the absorption of carbon dioxide for photosynthesis, transpiration is a constant concomitant of photosynthesis. In other words, the conditions that are necessary for photosynthesis make transpiration unavoidable. Transpiration is, strictly speaking, not a process of the plant itself but the result of the action of external conditions on the plant.

Some water is lost from the epidermal cells. This is known as *cuticular transpiration*. The amount of water given off in this manner is, however, small as compared with that which diffuses out of the stomata.

**Demonstration.** That water is lost by transpiration can be demonstrated by the arrangement shown in Fig. 41. A branch is

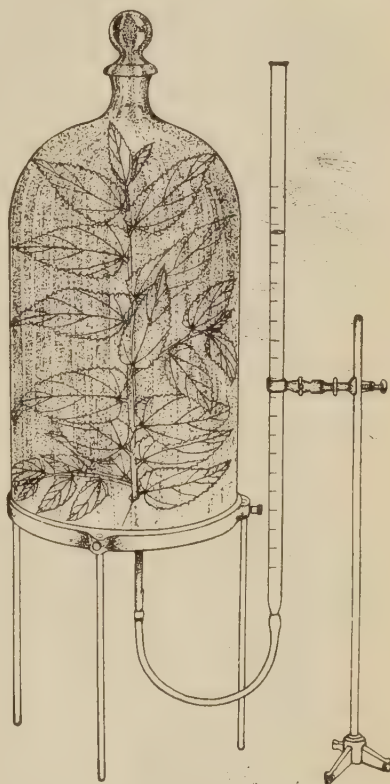


FIG. 41. Apparatus for demonstrating the loss of water by transpiration

attached, by means of a rubber tube, to a burette containing water. The branch is then placed inside a bell jar, when some of the water that is transpired will condense on the sides of the jar. A potted plant may be used in place of the branch. This experiment can be checked by setting up a similar preparation with a dead, dry branch substituted for the living one. In this

case no water will collect on the sides of the bell jar.



FIG. 42. Apparatus for measuring the amount of water absorbed by a transpiring branch

The amount of transpiration can be roughly determined in the manner shown in Fig. 42. A branch is attached, by means of a rubber tube, to a burette containing water. As transpiration continues water is absorbed from the burette, the amount being shown by the change in the height of the water in the burette. This method is inaccurate, as it measures the amount of water absorbed rather than that given off, and, moreover, the transpiration of a severed branch is frequently very different from that of a branch on the plant. A more accurate method of measuring transpiration is by weighing. A potted plant can be used for this purpose. The pot and soil should be sealed in a waterproof covering so that water

can evaporate only from the plant itself. The rate of transpiration can then be determined by weighing the preparation at definite intervals of time.

**Harmful effects of transpiration.** The most conspicuous effect of transpiration is the damage that results from excessive loss of water. If water is lost in transpiration faster than it is supplied from the roots, the leaves wilt; and if the excess of loss over supply continues, the plant will finally die. Even without actual wilting, the growth of plants may be greatly retarded by high rates of transpiration accompanied by a low moisture



content of the soil. This condition is very evident in many crops during long dry seasons. Delicate plants, such as many ferns, cannot grow in dry places, because they lose more water by transpiration than they can absorb from the soil. The bareness of desert regions is due to excessive evaporation and the scarcity of water in the soil. If it were not for the high rate of evaporation, however, there would be enough water in the soil in many desert regions to support a fair growth of vegetation at all times.

Excessive loss of water is one of the greatest dangers to which many plants are exposed, and is one of the most frequent causes of the death of plants. The harmful effects of excessive transpiration account for the fact that the leaf is protected by a heavily cutinized epidermis and by stomata which close as the result of the loss of water.

**Transpiration and temperature.** The evaporation of water has the effect of cooling the object from which it evaporates, and so the transpiration of water from plants tends to reduce their temperature. This fact explains why living leaves remain relatively cool when exposed to intense sunlight, while dry objects, such as paper, become hot. If it were not for this cooling effect of evaporation, leaves would be overheated on hot, sunny days. Animals, like plants, may be benefited by the cooling effect of evaporation. The reason why we feel cool when in front of an electric fan is that the wind increases the rate of evaporation of water from our bodies.

One danger of high leaf temperature is illustrated by the injury known as scalding. On hot days this injury sometimes results from the heating effect of intense sunlight following a shower which has left a high percentage of moisture in the air. The humidity lowers the rate of transpiration, with the result that the leaf becomes overheated. The injurious effects of high temperatures are, however, not confined to such conspicuous injuries as the one just mentioned. Many physiological processes, including growth, are affected by excessive heat.

**Transpiration and mineral matter.** When the chlorenchyma cells of the leaf lose water through transpiration, the osmotic

pressure in them is increased. This increase in osmotic pressure results in the diffusion of water from the xylem of the veins to the chlorenchyma, to replace the water lost by transpiration. The xylem is continuous from the leaf, through the stem, to those parts of the roots where water is absorbed. In the xylem water moves, not by diffusion, but as a steady stream through long tubes composed of dead cells. This stream of water carries the dissolved mineral matter along with it to the veins of the leaf, where both the water and the mineral matter can diffuse into the cells of the chlorenchyma. The movement of salts from the veins into the chlorenchyma, being by diffusion, is independent of the passage of the water but dependent on the relative concentration of the particular kind of matter in the chlorenchyma cells and in the veins. The reason why the kinds of mineral matter that are used in the leaves continue to diffuse into the chlorenchyma is that in their assimilation they are combined with other compounds and are thus changed to different substances. When a given substance combines with another to form a new compound, the concentration of the original substance is decreased. Owing to this fact a substance which is in solution in the xylem of the veins will continue to diffuse into the chlorenchyma as long as it is used by being combined with some other compound. The importance of transpiration in the passage of mineral matter into the leaves is that transpiration causes a stream of water to pass through the xylem and that this water carries dissolved material into the veins, where it can diffuse into the chlorenchyma.

The rate of the movement of mineral matter into the leaves is not necessarily proportional to the rate of transpiration, as the movement of dissolved material from the xylem into the chlorenchyma is by diffusion and depends on the relative concentration of the particular dissolved material in the two tissues, while the entrance of dissolved substances into the root is also by diffusion and depends on the relative concentration in the soil and root. Actual experiments indicate that under ordinary conditions there is little relation between rates of transpiration



and the amount of mineral matter in plants. It would appear that plants are frequently subjected to higher rates of transpiration than are necessary for the movement of sufficient dissolved material through the xylem.

While some transpiration would appear to be beneficial, particularly to tall plants, because it accelerates the movement of dissolved material from the roots to the leaves, there are at least many small plants for whose development it would seem to be unnecessary, as is shown by the fact that they will grow in an atmosphere kept as nearly saturated with water as is possible even under experimental conditions. In the absence of transpiration the movement of dissolved materials can take place through the plant slowly by means of diffusion.

**Factors influencing transpiration.** The rate of transpiration varies greatly with changes in the environment. The factors that affect transpiration are the same as those that influence the rate of evaporation in general.

The effects of light, heat, wind, and humidity on ordinary evaporation are matters of common knowledge. We know that if we put a wet handkerchief in a warm place it will dry much more rapidly than it would in a cold place. The drying of the handkerchief is, of course, simply the evaporation of water from the handkerchief. We know also that wet clothes will dry more rapidly in sunlight than in a dark or shaded place, and, other conditions being equal, more rapidly on a windy day than on a still day. Likewise they will dry more rapidly on a dry day than on a very moist one.

Transpiration varies with the temperature, because water vaporizes more rapidly at high temperatures than at low temperatures, and because warm air absorbs more moisture than cool air does. Light increases transpiration, owing to the heat produced by the light. Wind increases transpiration in two ways: Diffusion of water vapor from the stomata tends to saturate the atmosphere around the leaves; wind removes this moist air and replaces it by drier air. Wind also, by causing the leaves to shake and bend, increases the movement of gases in the intercellular

spaces. Again, the rate of transpiration is greatly influenced by the humidity of the air, that is, the amount of water vapor in the air. Dry air not only absorbs more moisture than wet air does but absorbs it more rapidly. Therefore the rate of transpiration decreases with rising humidity.

**Control of transpiration.** The rate of transpiration is greatly influenced not only by external conditions but also by the

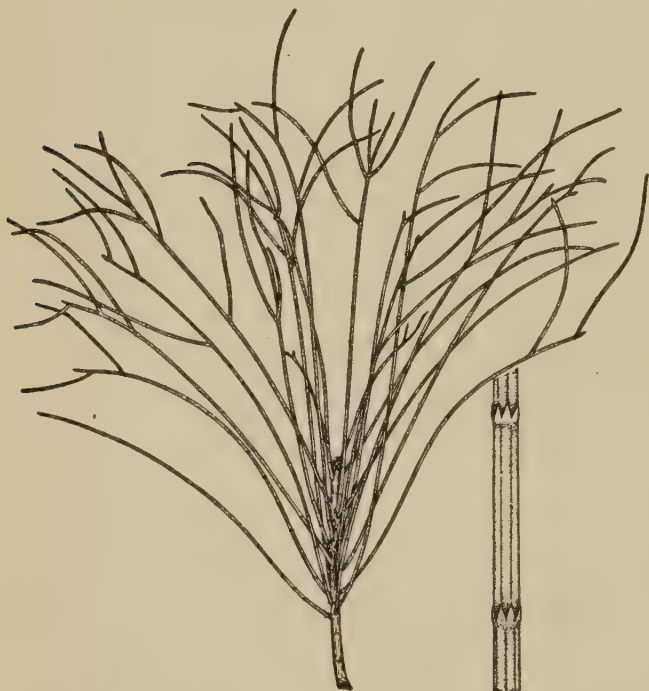


FIG. 43. Branches of *Casuarina* with scale-like leaves. ( $\times \frac{1}{3}$ )

The small figure on the right shows a piece of a branch with whorls of scalelike leaves at the nodes

plants themselves. This is brought about in two general ways: by *permanent morphological changes* which restrict or accelerate the rate of transpiration, and by *physiological changes* which control the rate temporarily.

**Restriction of transpiration.** Among the structural modifications which may influence the rate of transpiration are the number and size of the leaves, the thickness of the leaves, the compactness of the chlorenchyma, the number and arrangement of the stomata, the thickness

and cutinization of the epidermal walls, and the development of trichomes (outgrowths from the epidermal cells).

**Number and size of leaves.** Other things being equal, the amount of water transpired by a plant will tend to vary with the number and size of its leaves, as the more surface the plant has for transpiration the more water it can transpire. It is not surprising, therefore, to find that most plants growing in moist regions have a large number of fair-sized leaves. When the leaves are few in number they are usually large. On the other



hand, plants growing in an arid region will usually have few and small leaves, so that the rate of transpiration is restricted by a reduction in the transpiring surface.

Gardeners, when transplanting large plants, very commonly reduce the number of leaves, to restrict transpiration. In removing a plant from the soil the parts of the roots which absorb water are destroyed to a very considerable extent. The plant can therefore absorb less water and so has less water for transpiration. In order to balance this effect it is a usual practice to remove a considerable portion of its leaves.

**Thickness of leaves.** If the leaves of a plant are thick, they will have a smaller outside area per unit of volume than they would have if they were thin. Therefore thin leaves will transpire more per unit of volume than will thick leaves. In keeping with this fact we find that plants growing in very moist places usually have thin leaves, while those which are exposed to dry conditions have thicker leaves.



FIG. 44. A branch of an Australian desert plant, *Hakea*, with the leaves modified as spines. ( $\times \frac{1}{2}$ )

**Compactness of chlorenchyma.** If the cells of chlorenchyma are arranged close together, there will be a less free circulation of gases inside the leaf than there would be if the cells were loosely arranged, with large intercellular spaces; consequently, the more the spongy chlorenchyma is replaced by palisade the more the rate of transpiration will be restricted. The relative development of the palisade and the spongy chlorenchyma cells varies greatly under different environmental conditions. In very moist places, as in damp, shaded ravines, the spongy chlorenchyma usually occupies a larger portion of the leaf than does the palisade, and not infrequently the palisade disappears

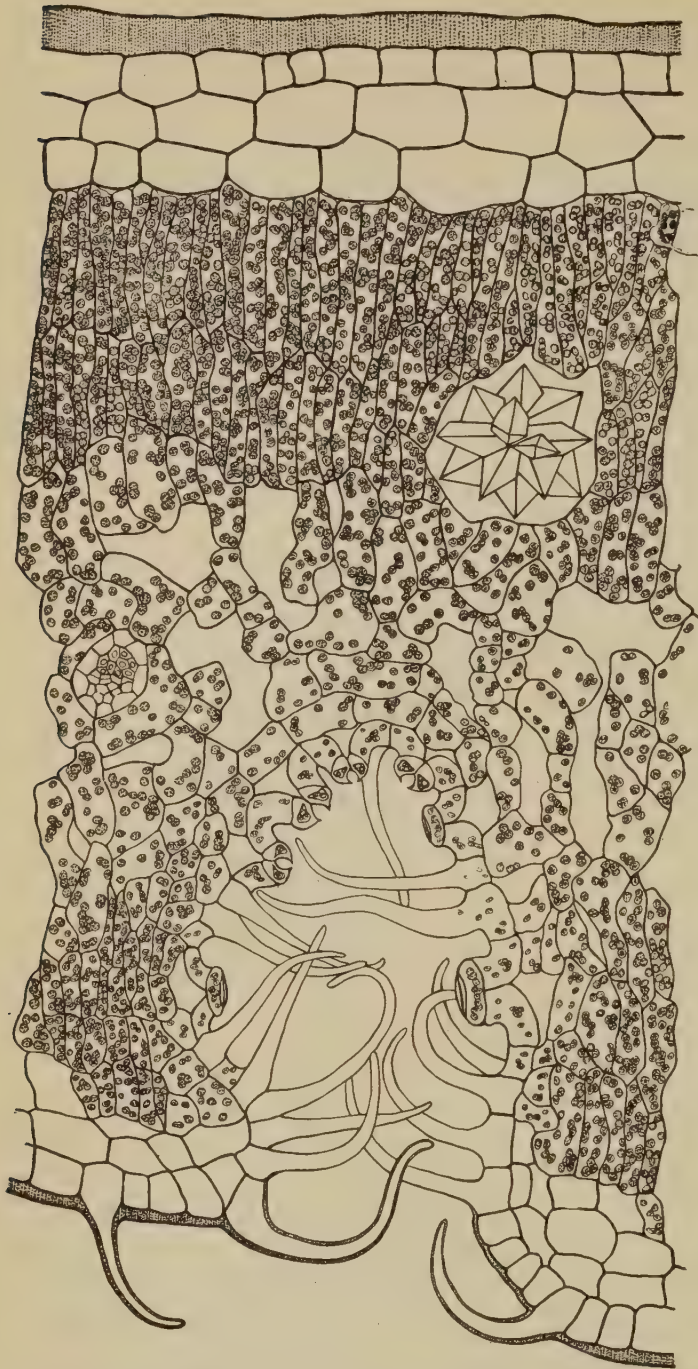


FIG. 45. Cross section of a leaf of oleander (*Nerium*) with upper and lower palisade, three-layered upper epidermis, and stomata in a pit protected by trichomes. ( $\times 285$ )

entirely (Fig. 450). In dry regions the reverse is the case. Here the spongy chlorenchyma is usually less conspicuous than the palisade. There may be a thin layer of spongy chlorenchyma near the lower epidermis; or the layer of spongy chlorenchyma may be between two layers of palisade (Fig. 45), one below the upper epidermis and the other just above the lower epidermis; or, again, the spongy chlorenchyma may be entirely replaced by palisade chlorenchyma. Note the difference in the development of the palisade and the spongy chlorenchyma as shown in Fig. 35 and also in Figs. 24 and 26. The relative development of the palisade and the spongy chlorenchyma may be suited not only

to various rates of evaporation but also to various intensities of light. In damp ravines the light is usually of low intensity, and in such situations not much light would be likely to pass through thick layers of tissue. On the other hand, in dry regions the



atmosphere is likely to be clear and the intensity of light to be very great. Under such conditions light sufficient for photosynthesis would penetrate through a much thicker layer of tissue than would be the case with plants exposed to lower intensities of light.

**Number and arrangement of stomata.** The rate of transpiration will naturally vary with the number of stomata. Plants growing in moist situations are likely to have more stomata per unit of area than those in dry regions. Some plants which are natives of arid localities have stomata that are sunk in pits (Figs. 45, 46), while some which are found in moist regions have their stomata raised above the general level of the epidermis. More water will naturally be transpired through exposed than through protected stomata.

**Thickness and cutinization of epidermal walls.** The chief function of the epidermis is to restrict the amount of transpiration by means of its thick and cutinized outer walls. The amount of transpiration will, of course, decrease as the thickness and the cutinization of the wall increase. Plants growing in dry situations have thicker epidermal walls than those in moist regions. Even on the same plant, leaves exposed to the sun have thicker epidermal walls than those in the shade (Fig. 35). Xerophytic plants may have not only thick epidermal walls but also an epidermis composed of more than one layer of cells (Fig. 45).

**Development of trichomes.** Many leaves have hairs on their surfaces. These hairs are outgrowths from the epidermal cells and are frequently dead. If such dead hairs are numerous and

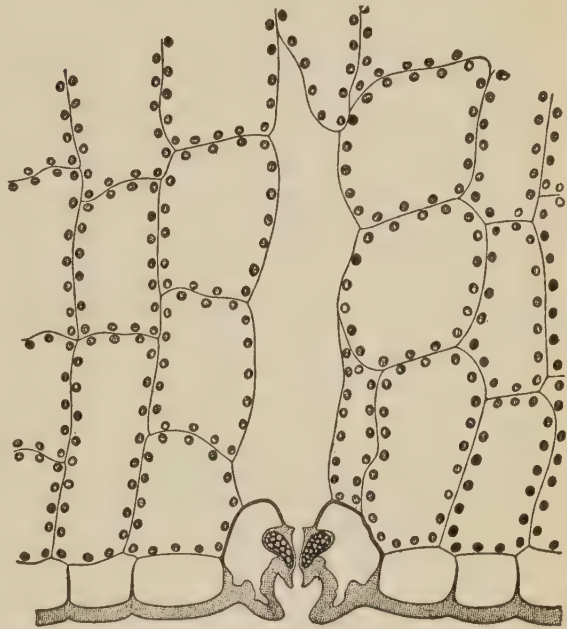


FIG. 46. Cross section of a portion of a leaf of a century plant (*Agave cantula*), showing a sunken stoma. ( $\times 170$ )

close together, they will have a tendency to decrease the rate of transpiration, as they tend to minimize the effect of the movement of air near the stomata.

**Hereditary and acquired modifications of structure.** The changes in structure which restrict or accelerate the rate of transpiration are of two general classes: those changes which are characteristic of a species and are hereditary, and those which are acquired by individual plants or leaves in response to the condition under which they are grown.

**Acquired modifications.** Even on the same plant some leaves may be more exposed than others to the effects of evaporation, as they are not all equally exposed to the action of sun and wind. We usually find that on the same plant the leaves that grow in the sun are thicker and have more compact chlorenchyma and thicker epidermal walls than those that grow in the shade (Fig. 35). These differences are due to the response of the individual leaves to their environment. A practical application is made of this fact in growing tobacco under shade in order to obtain large, thin, and pliable leaves to be used as cigar wrappers. While leaves respond, to a certain degree, in the ways mentioned above, the possible extent of such response is limited.

**Hereditary modifications.** Besides the response of individual leaves and plants to different environments there are hereditary modifications of leaf structure which may be more pronounced and which fit plants for different environmental conditions. On many desert plants the leaves are reduced to rudimentary structures or are modified into spines (Figs. 43, 44, 512). No matter under what conditions these plants may be grown, they will not develop large leaves. Likewise, delicate ferns will not develop leaves which can resist the high rates of evaporation that occur in desert regions. Plants which are natives of the desert and have very small leaves may, if grown in moist regions, develop somewhat larger leaves, but they will never develop leaves of any great size. While environment may have a marked influence on leaves, heredity is in general more important than environment in determining their size.



Fig. 47, which represents a cross section of a leaf, shows an interesting hereditary modification suited to a particular kind of environment. The thick, water-storing epidermis helps the plant to endure short periods of comparative dryness, while the single layer of chloroplastids indicates a shady habitat.

**Effect of evaporation on distribution of plants.** In nature we find that plants of desert, fairly moist, and very moist regions are all specially fitted for the conditions under which they grow, and that the structural modifications which fit them for their native localities are fixed by heredity to such an extent that usually they will not thrive under conditions that are very different from those of their natural habitat. The rate of evaporation is one of the most important environmental factors for which plants are fitted, and the rate of evaporation determines, to a considerable extent, the kinds of plants which grow naturally or can be cultivated profitably on any given area. If the soil is sufficiently irrigated, many crop and garden plants which are suited to fairly moist conditions can be grown successfully in regions that are naturally dry; but there are many plants which cannot withstand the very high rates of evaporation prevailing in arid regions, no matter how much water is in the soil. Many desert plants can stand much more moist conditions than those under which they normally occur, and can be successfully cultivated in moist regions; but when left to themselves they are not able to compete with the vigorous plants of moist areas.

High rates of evaporation, accompanied by a small percentage of water in the soil, result in an open growth of small

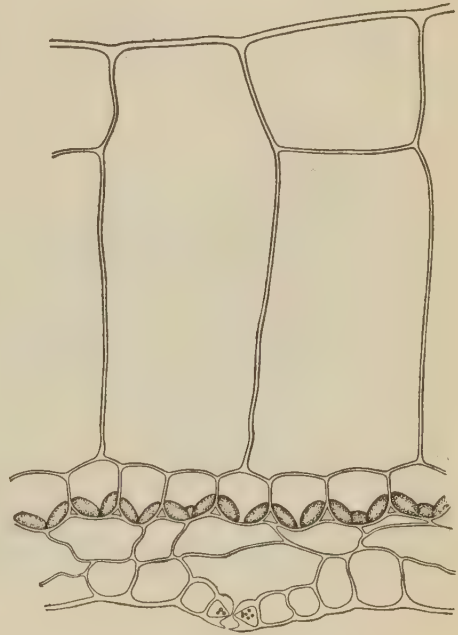


FIG. 47. Cross section of a leaf of *Peperomia pellucida*, a tropical plant that thrives on shady stone walls

Note water-storing upper epidermis and single layer of cells with chloroplastids

plants (Figs. 48, 511-513); low rates of evaporation and abundant moisture in the soil, other conditions being favorable, bring about a dense forest of tall trees (Figs. 6, 488).

**Regulation of transpiration.** The rate of transpiration is regulated more or less temporarily in a number of different ways. The most important of these are by deciduous leaves, by drying of the walls of the chlorenchyma, and by opening and closing



FIG. 48. Desert region in Arizona with *Yucca alata* to the left and *Prosopis velutina* to the right

of stomata. There are also some other means, such as rolling and folding of leaves, which reduce the transpiring surface.

**Deciduous leaves.** Broad-leaved trees which grow in regions that have either a very cold or a very dry season usually shed all their leaves during such periods of cold or of drought. Of course the shedding of the leaves greatly restricts transpiration.

When the weather is very cold, plant roots can absorb little water from the soil, while if the leaves were exposed to the air, they would continue to transpire. This is one of the reasons why broad-leaved trees in the colder parts of the temperate zone shed their leaves at about the beginning of the cold season (Fig. 496).

A very similar result ensues when trees are subjected to a long, pronounced dry season. At such times both the soil and



the air will usually contain comparatively little moisture, with the result that if trees had an extensive leaf area, their roots could not absorb enough water to supply that which would be lost by transpiration. The shedding of leaves by plants of the



FIG. 49. Surface view of a stoma of Wandering Jew (*Zebrina pendula*).  
( $\times 145$ )

temperate zone during the autumn, and by tropical plants which grow in regions with a pronounced dry season, is therefore the result of very similar circumstances. In tropical regions where there is no pronounced dry season, plants retain their leaves throughout the year.

lose more water than the roots can absorb. The result of this is that the cells, and also the cell walls, then contain less water than when transpiration is less rapid. Very wet substances naturally lose more water than drier ones; and so, as the cell walls become drier, less water diffuses from them into the intercellular spaces. The rate of transpiration is thus automatically lowered.

**Opening and closing of stomata.** A stoma is an opening between two sausage-shaped cells called *guard cells*. Fig.

49 shows a view of a partly open stoma, and Fig. 50 a cross section through a closed stoma and surrounding cells. The guard cells are constructed in such a way that they can move so as to open and close the stoma. Stomata are usually closed at

**The drying of chlorenchyma walls.** On hot, dry, sunny days the leaves of plants may

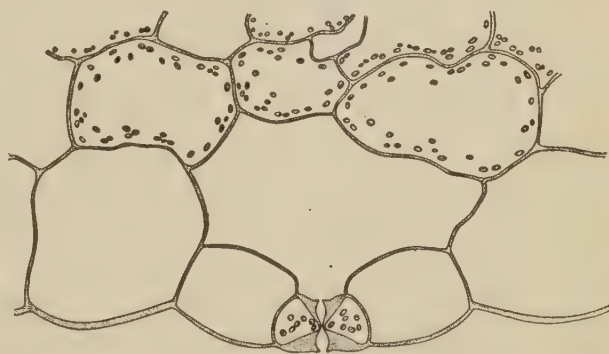


FIG. 50. Cross section of a stoma and surrounding cells of *Zebrina pendula*.  
( $\times 130$ )

night and open in the day; but when the rate of evaporation is rapid, they also close during the day. When the guard cells are turgid the stomata are open, while as the guard cells lose their turgidity the stomata close.

**Mechanism of opening and closing of stomata.** To understand how changes in the turgidity of the guard cells cause the opening and closing of the stomata it will be necessary to study the structure of the guard cells. There are a number of types of guard cells, but for simplicity we may consider only what is



FIG. 51. Combined cross section and surface view of a stoma

probably the most widely distributed one. A transverse section through a guard cell (Fig. 50) shows that the wall which is farthest from the stomatal pore (dorsal wall) is very thin, while that which is next to the pore (ventral wall) is much thicker. When the guard cells become turgid their walls naturally tend to stretch; but

the ventral walls, owing to their great thickness, stretch much less than do the dorsal walls. The result is that the cells become bent, with the concave side toward the pore. This is the principal cause of the opening of stomata. When the guard cells lose their turgidity they straighten out and come together, thus closing the stomata. This type of bending can be illustrated by means of a rubber tube or an elongated toy balloon, to one side of which adhesive tape has been attached. When the tube is inflated it will bend, the side to which the adhesive tape has been applied being the concave side (Fig. 52).

The ventral wall is not uniformly thickened. In the center, as seen in cross section, it is thin. Away from the center it is greatly thickened, and along the edges it projects into the stomatal pore. The central part of the wall also bulges into the pore. The stomatal pore is thus not of uniform diameter, but consists of two more or less inclosed chambers which are



connected by means of a narrow passage. The fact that the ventral wall is composed of two thickened ridges connected by a thin strip has distinct advantages. These ridges are so thick that they offer resistance to any tendency to stretch them, so that when the cell becomes turgid and the thin dorsal wall is stretched, the thin part of the ventral wall bends and there is a tendency for it to be drawn away from the center of the stomatal opening, thus enlarging that opening. This type of movement can be imitated roughly by means of two boards fastened together at one end by a piece of leather to represent the thin part of the ventral wall, and at the other end by a rubber band to represent the dorsal wall (Fig. 53). If the rubber band is stretched, it will be seen that the other ends of the boards are drawn to it. When the guard cell loses its turgidity, the dorsal wall contracts and the thin part of the ventral wall bulges out, and it is this part which closes the stomatal passage. It is an advantage to have the passage closed by the thin part of the ventral walls (Fig. 50), as thin walls can be pressed much closer together than could thick, rigid ones.

**Factors affecting opening and closing of stomata.** The guard cells contain well-developed chloroplasts, while these are usually not present in the other cells of the epidermis, except in some plants that grow in moist, shady situations. During the day the contents of the guard cells have a high osmotic pressure. Consequently, when the surrounding cells are well supplied with water, the guard cells draw water from them and become turgid, and the stomata open. If, however, the

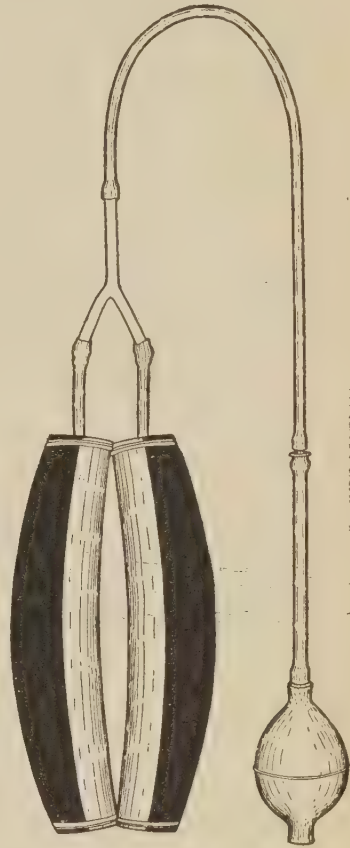


FIG. 52. Apparatus to imitate the opening and closing of a stoma

The two large rubber tubes with adhesive tape on the adjacent sides are inflated by means of the rubber bulb

plant loses more water from its leaves than is absorbed by its roots, the water content of the cells of the leaf, including the guard cells, is lowered and the guard cells become less and less turgid. As this process continues the stomata close. The rate of transpiration is regulated to a considerable extent by the opening and closing of stomata. The closing of stomata does not, however, entirely stop transpiration, as a small amount of

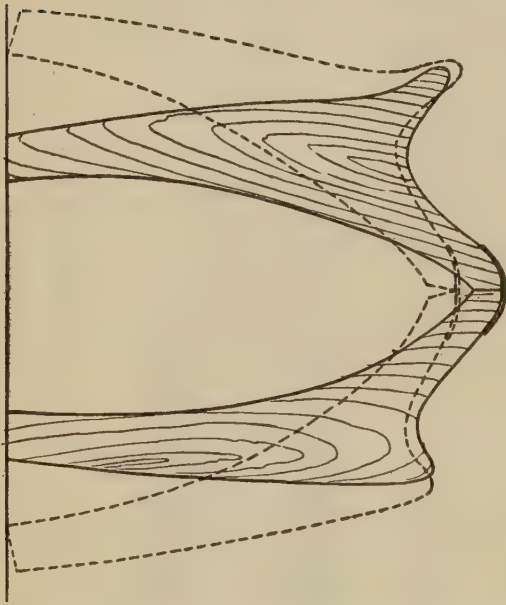


FIG. 53. Arrangement to imitate the bending of the ventral walls of a stoma

transpiration takes place through the cuticle of the epidermal cells.

#### Daily march of transpiration.

The rate of transpiration is dependent to a considerable extent on the rate of evaporation. Therefore we shall consider first the variations in the rate of evaporation at different times during the day and night. During the night the rate of evaporation is usually very low, as at this time the air is much colder than during the day and the accelerating influence of sunlight is absent. The air is also much more nearly saturated with water during the night than dur-

ing the day, as cold air can hold less water than warm air. Thus, although there may be the same amount of water in the air during the day and during the night, the air becomes more and more saturated as it cools during the night. We see the result of this phenomenon in the formation of dew, which is the result of the condensation of water from the air. This condensation takes place at night because the air is more nearly saturated at that time than during the day. The increase in the saturation during the night has a great retarding effect on the rate of evaporation. With the coming of daylight the rate of evaporation increases, owing to light, greater heat, and the fact that the air becomes less saturated with water as it



gets warmer. This increase in the rate of evaporation usually continues on bright days until some time in the afternoon. As the sun goes down the rate decreases, and the decrease continues until the low night rate is reached.

If the rate of evaporation is comparatively low during the day, the rate of transpiration may follow that of evaporation rather closely. But when the rate of evaporation during the day increases to a point where transpiration is excessive, the rate of transpiration is restricted by the movements of the guard cells and the drying of the chlorenchyma walls. Thus it frequently happens that while the rate of evaporation continues to increase until some time in the afternoon, the highest rate of transpiration is reached in the morning. At night the rate of transpiration is low, owing to the very low rate of evaporation and to the closing of the stomata.

**Water content of the leaf.** Many leaves contain from 80 to 90 per cent of water. When, on a dry day, a plant loses more water than it absorbs, the water content of the leaves naturally diminishes; thus it very frequently happens that leaves contain less water during the middle of the day than during the night. In many plants the loss of water goes so far on dry days as to cause an actual wilting of the leaf. Not only leaves but other parts of plants frequently contain less water during the day than at night. It is for this reason that vegetables have a crisper and fresher appearance when picked early in the morning than when gathered later in the day.

The relation of moisture to number and size of leaves has been treated in a previous paragraph.

### SHAPES OF LEAVES

While most leaves have petioles, many do not possess them. Leaves without petioles are *sessile*. The petiole is usually attached at the edge of a leaf, but may be attached on the lower surface within the margin (Fig. 54). In the latter case the leaf is *peltate*.



FIG. 54. Peltate leaf of castor-oil plant (*Ricinus communis*). ( $\times \frac{1}{4}$ )

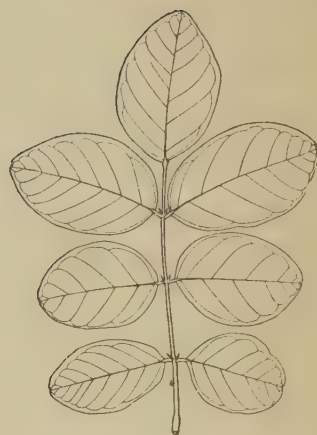


FIG. 55. Pinnate leaf (*Clitoria ternatea*). ( $\times \frac{1}{3}$ )



FIG. 56. Bipinnate leaf of rain tree (*Enterolobium saman*). ( $\times \frac{1}{4}$ )

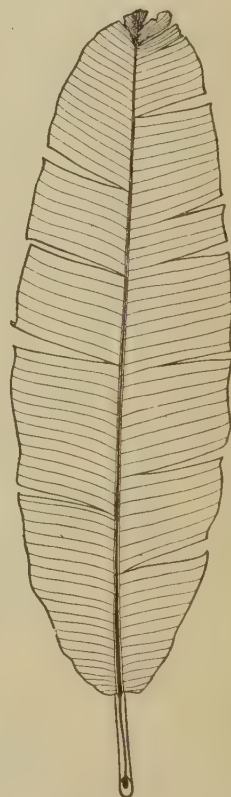


FIG. 57. Leaf blade of banana. ( $\times \frac{1}{17}$ )



Leaves are *simple* when there is only one blade, and *compound* when there is more than one. When the *leaflets* of a compound leaf are arranged on the side of a common axis (*rachis*), the leaf is *pinnate* (Fig. 55) and the leaflets are called *pinnae*. If the main divisions are again once or twice pinnate, the leaf is *bipinnate* (Fig. 56) or *tripinnate*.

One advantage of compound leaves is that they do not offer as much resistance to the winds as do entire leaves, and so need less strengthening tissue to protect them from being torn. The huge entire blades of the banana (Fig. 57) show an interesting modification in that they are not greatly strengthened but instead have certain weak structural lines where the leaf can be torn by the wind without any particular damage to the plant.

Plants having unbranched stems must have large leaves if they are to expose an extensive surface to the light. In keeping with this fact we find that large palms and tree ferns have enormous leaves. On the other hand, plants with many small branches have small leaves.

The general shape of leaves is related to their arrangement on the stem. When leaves are densely crowded they are usually *linear* (long and narrow), and so shade each other much less than would broad leaves. When less crowded the leaves are more often somewhat oval in outline, and when spread out they are apt to approach a circular shape.

When leaves are lobed, the lobing follows the large veins (Fig. 58), so that the photosynthetic tissue is nearer the principal veins than would be the case if the leaves were entire.



FIG. 58. Lobed leaf of papaya (*Carica papaya*). ( $\times \frac{1}{8}$ )

## TRICHOMES

Some of the epidermal cells of most plants grow out singly or, less frequently, in groups, to form appendages which are known as *trichomes* or hairs. Frequently the trichomes lose their protoplasmic contents and become filled with air. The young leaves of many plants have trichomes which are shed as the leaf becomes older. Cotton consists of long unicellular hairs which grow from the epidermis of cotton seeds.

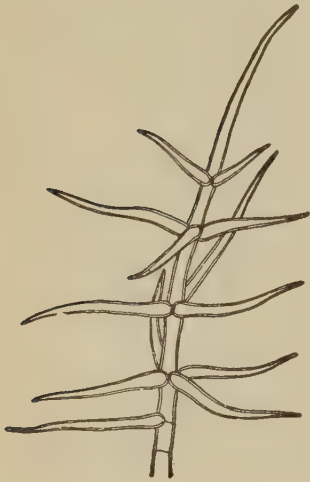


FIG. 59. Branched hair of *Callicarpa caudata*.  
( $\times 50$ )

Even the simple unbranched hairs show great variety. They may be unicellular or multicellular, straight or curly, project straight from the epidermis or lie parallel with it. When they lie against the surface of the leaf and all point in the same direction, they produce a silky appearance. The methods of branching exhibited by the trichomes are very diverse. Among the most beautiful forms of trichomes are those known as scales. These are flat structures having short central stalks



FIG. 60. Top and side views of stellate hair of *Callicarpa erioclona*. ( $\times 350$ )

(Fig. 61). Scales are sometimes found so close together as to form an almost complete covering over the surface of a leaf.

A dense covering of dead trichomes has a tendency to restrict the rate of transpiration. The transpiration of a leaf in still air brings into being a layer of moist air around the leaf, and the



diffusion of water from the leaf into this moist air is less rapid than it would be into dry air. When there is free movement of air around the leaf, wind will replace the moist air with drier air. A dense layer of trichomes tends to reduce the movement of the air and so to lower the rate of transpiration.



FIG. 61. Scale of *Elaeagnus philippensis*. ( $\times 75$ )

Hairs are usually most numerous on the under, or stomata-bearing, surface of the leaf. While a dense covering of trichomes retards transpiration, the

hairs of many leaves appear to be too scattered to have any appreciable effect.

A covering of hairs, by holding a layer of air near the leaf, may prevent water from reaching and clogging the stomata. When a leaf with such a coating of trichomes is submerged in water, the layer of air near the epidermis glistens with a silvery sheen. Although

submerged, the epidermis may remain dry for a considerable length of time. Even such short trichomes as those shown in Fig. 35 may be very effective in keeping water from the stomata. While trichomes may restrict the rate of transpiration, they not only do not interfere with the diffusion of carbon dioxide into the leaf but may

FIG. 63. Stinging hair of a nettle (*Laportea meyeniana*). (Central drawing  $\times 150$ )



actually assist in keeping open a passageway for this diffusion when the stomata might be clogged as the result of rain or dew.



FIG. 62. Bristlelike hair of cowitch (*Mucuna pruriens*). ( $\times 30$ )

**Bristlelike hairs.** A number of plants possess stiff, sharp-pointed, bristlelike hairs which readily penetrate the skin of man and produce very disagreeable effects. Some of these hairs have

barblike protuberances along their sides (Fig. 62). These protuberances increase the irritating effect of the trichomes. Bristlelike hairs may afford protection to plants by keeping animals from eating the leaves, but comparatively few plants have hairs stiff enough to be very effective in this way.

**Stinging hairs.** Stinging hairs are one of the most interesting types of trichomes (Fig. 63). A typical stinging hair contains a poisonous liquid and consists of a basal bulb-shaped portion from which projects a stiff, slender, tapering structure that ends in a small knob or a sharp point. Near the tip there is usually an oblique thin place in the wall, so that when the body of an animal or some other object is pressed against the tip with sufficient force, the tip is broken off, leaving a sharp point that can readily penetrate an animal's skin. The wall of the rounded basal portion is distended by the pressure of the contained liquid,

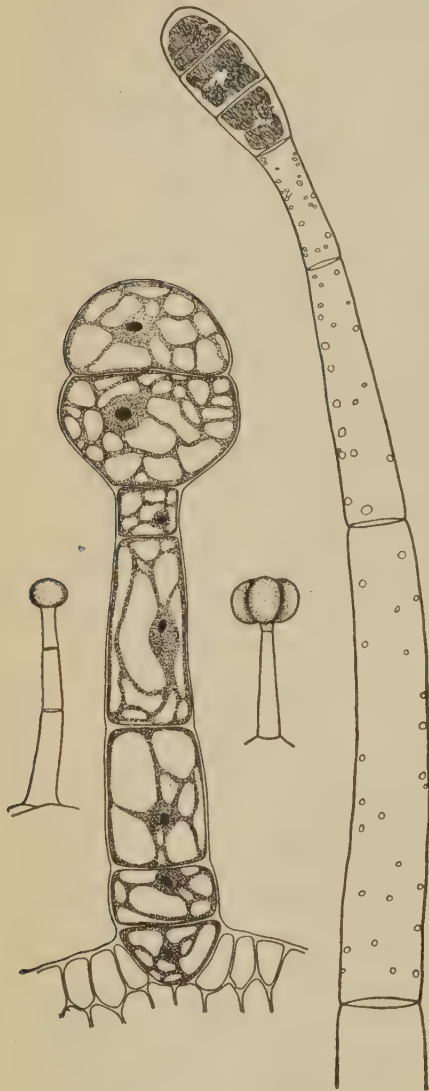


FIG. 64. Glandular hairs

Left, water hyacinth; second figure, squash; third figure, tomato; right, tobacco. ( $\times 200$ )

and it contracts when this pressure is removed by the breaking of the tip. This contraction tends to force the fluid through the opening in the tip, so that an animal into which the sharp point has stuck will be injected with the poisonous fluid. The pressure of the animal against the hair also helps to force the liquid from the bulbous base.



**Glandular hairs.** A great variety of plants have glandular hairs (Fig. 64). These secrete oil, resin, or mucilage. A typical glandular hair consists of a stalk and an enlarged terminal portion, which is the gland proper. This may be unicellular or multicellular. The strong odors of many plants are due to the excretions of glandular hairs.

### SPECIALIZED LEAVES

The principal function of ordinary foliage leaves is photosynthesis. Besides the primary function of foliage leaves they also perform such functions as respiration and growth, which are common to all living plant parts.

In addition we find that many leaves are specially modified to perform functions which are not usually the principal ones of leaves, or are modified to carry on the principal function in an unusual manner. Such leaves may be called specialized leaves. As examples of leaves which per-



FIG. 65. Leaves showing bladelike petioles

Left, Philippine grapefruit (*Citrus decumana*) ( $\times \frac{1}{3}$ );  
right, *Quassia amara* ( $\times \frac{1}{4}$ )

form the primary function of leaves in an unusual manner we may mention such leaves as those of oranges and lemons, where the petiole has a bladelike structure and is especially fitted for photosynthesis (Fig. 65), and the stipules of the garden pea (*Pisum sativum*), which are bladelike and have the functions of

a blade (Fig. 69). The special functions for which some leaves are particularly suited may be grouped under six headings: *support* (stem function), *absorption* (root function), *attraction of insects* (floral function), *reproduction* (seed function), *storage*,



FIG. 66. Banana plant. ( $\times \frac{1}{42}$ )

and *protection*. These functions may be subsidiary to the ordinary functions of leaves, or be more important, or even replace the usual functions.

**Support (stem function).** The primary function of stems is to support the aërial parts of the plants. This function is performed by four special types of leaves: tendrils, which may be modified whole leaves or parts of leaves; leaves with hooks; leaves with floats; and leaves that have supporting leaf bases.

**Supporting leaf bases.** The leaf bases of the banana and other similar plants are greatly elongated and grow so close together as to produce a structure which has an appearance very much



like that of an ordinary trunk, and which supports the leaf blades and the fruit in much the same way as does a trunk (Fig. 66). The main stem is thick and short, with a convex top to which the leaf bases are attached. The slender fruiting stalk pushes up in the center of the elongated leaf bases and is supported by them (Fig. 67).

In grasses the younger part of the stem has a soft growing region just above the attachment of each leaf. This growing region is so soft and weak that it could not, by itself, support the part of the plant above it. The leaf base has the form of a long, slender tube which surrounds and supports the stem and enables it to bear its load (Fig. 68).

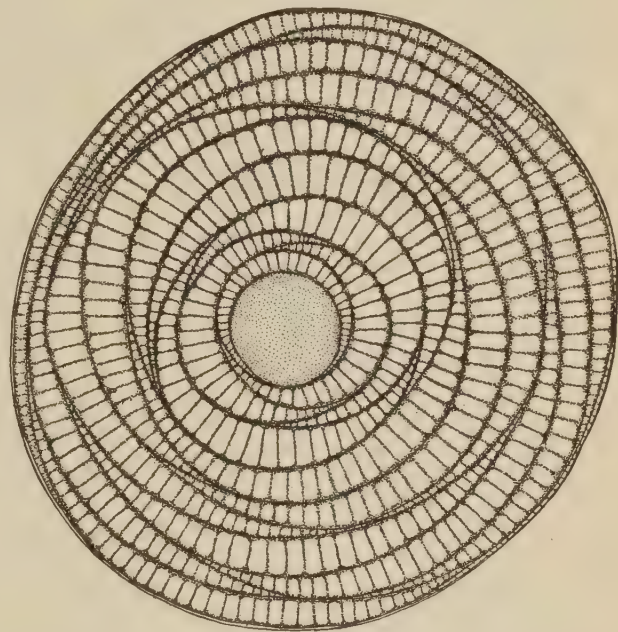


FIG. 67. Cross section of the false trunk of the banana plant, showing small flowering stalk surrounded by leaf bases. ( $\times \frac{1}{3}$ )

**Tendrils.** The climbing plants have slender stems which do not possess sufficient strength to hold themselves erect. Such plants catch on to other objects, particularly other plants, and thus make use of the strength of these other objects to support them. This enables them to grow up into the sunlight without expending the material which would be necessary to build a strong trunk. Tendrils are one of the means by which plants hold on to other objects. Tendrils are long, slender structures which curl around objects with which they come in contact. They are frequently, but by no means always, modified leaves. Any part of a leaf may be modified in this manner. Tendrils may be modified whole leaves, petioles (Fig. 69), leaflets as in the garden pea (*Pisum sativum*) (Fig. 69), tips of leaves (Fig. 69), or modified stipules (Fig. 69).

**Hooks.** Some climbing plants have leaves with hooks which enable them to hold on to other objects. Excellent examples are afforded by the climbing palms known as rattans (Fig. 489). These have large, feathery leaves with numerous curved, sharp, pointed hooks (Fig. 70) which catch on to objects with which they come in contact and thus support the stem and enable the plant to climb. Some climbing plants have stipular hooks which

serve the same purpose.

**Floats.** The floating plants develop very loose tissue with large air spaces (Fig. 71). Such tissue enables the plant to float on the surface of the water. The bulbous petiole of the water hyacinth is occupied largely by air spaces and presents a striking case of the development of floating tissue (Figs. 71, 72). Similar tissue is found in the blades of floating leaves (Fig. 5).



FIG. 68. Tip of stalk of sugar cane. ( $\times \frac{1}{30}$ )

The air spaces in plants serve for aëration, that is, the exchange of gases between the cells and the external atmosphere. Frequently the large air spaces in aquatic plants are primarily useful for this function, as is particularly true of the large air tubes which traverse the petioles of water lilies (Fig. 40) and by which the oxygen set free in the leaves by photosynthesis is allowed to diffuse to the roots.

**Absorption (root function).** One of the chief functions of roots is to absorb water as well as compounds of nitrogen and other elements which plants usually obtain from the soil. Most leaves are incapable, under ordinary circumstances, of absorbing these



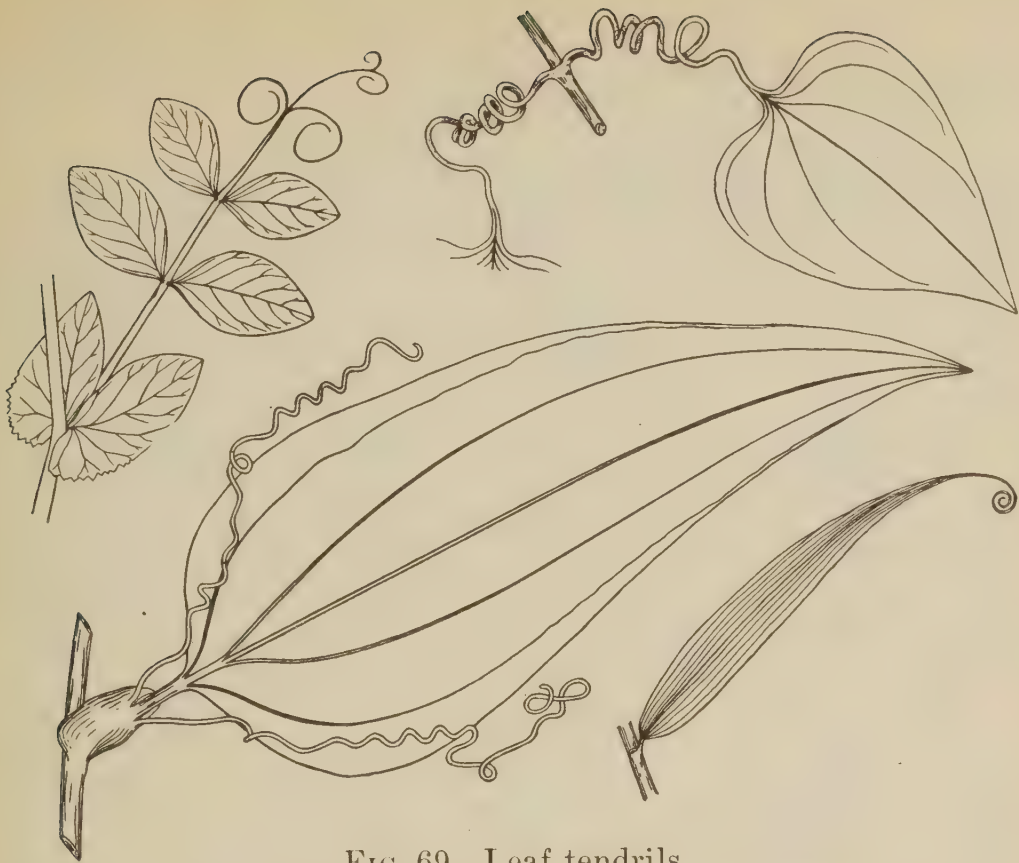


FIG. 69. Leaf tendrils

Upper left, *Pisum sativum* ; upper right, *Clematis smilacifolia* ; lower left, *Smilax leucophylla* ; lower right, *Flagellaria indica*. ( $\times \frac{1}{3}$ )



FIG. 70. Tip of a stem of a rattan palm (*Calamus*). ( $\times \frac{1}{38}$ )

Left, back of rachis ; right, back of extension of rachis

substances, but many plants have leaves which are especially fitted for this function. Such leaves fall rather naturally into

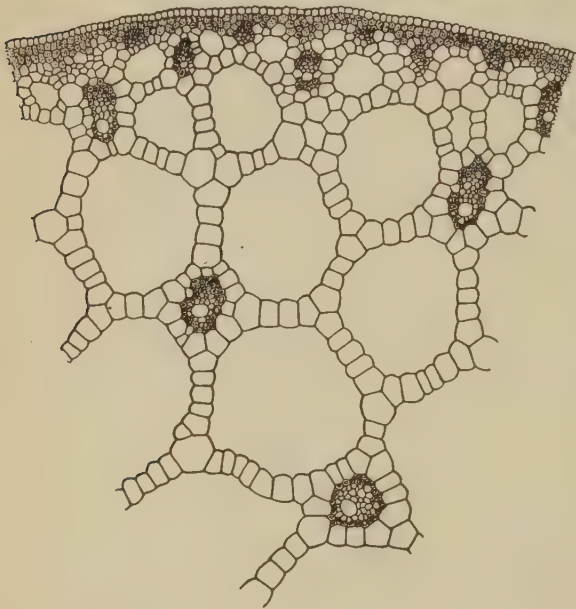


FIG. 71. Large air spaces in bulbous petiole of water hyacinth (*Eichhornia crassipes*). ( $\times 30$ )

two general classes: those especially fitted for absorbing water and the things which are ordinarily dissolved in it, and those that catch insects or other small animals and obtain nutrient substances in this manner. We may speak of these two classes of leaves as water-absorbing leaves and carnivorous leaves.

#### Water-absorbing leaves.

The leaves of submerged plants are not ordinarily exposed to evaporation and do not have cutinized epidermal walls. They are surrounded

by water in which mineral matter is dissolved, and so can absorb these substances directly.

Many plants growing in dry situations have leaves that are provided with absorbing hairs. These may be of great advantage to a plant by enabling it to absorb water from light rains which do not wet the soil, or even from dew. They are of considerable use to plants growing in situations where for long periods there may be dew every night but

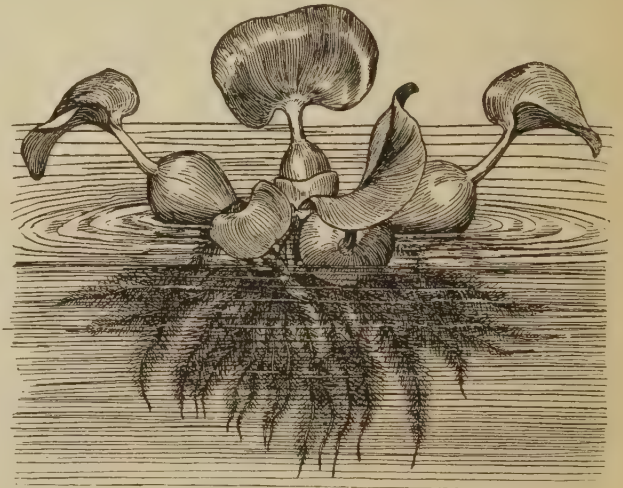


FIG. 72. Water hyacinth (*Eichhornia crassipes*) with petioles modified as floats. ( $\times \frac{1}{3}$ )

no rain. Dew is condensed on and absorbed by these hairs. Some plants have leaves which are especially fitted for collecting



and absorbing water. The bromeliads (plants of the pineapple family) furnish excellent examples of absorbing hairs (Fig. 490).

**Carnivorous leaves.** There are several kinds of leaves which catch insects or other small animals.

The pitcher plants have their leaves modified into pitchers in which water collects. The best-known pitchers belong to the temperate zone genus *Sarracenia* (Fig. 73) and the tropical genus *Nepenthes* (Fig. 74). The species of *Sarracenia* are rosette plants; that is, the leaves arise in a cluster from a very short stem. The species of *Nepenthes* are vines on which the pitchers are borne at the ends of long, tendril-like leaves. Insects are drowned in the water in the pitchers. In the pitchers of the genus *Sarracenia* the insects are decomposed by the

FIG. 73. Pitcher leaf of *Sarracenia*. ( $\times \frac{2}{3}$ )

action of bacteria, while the pitchers of the genus *Nepenthes* excrete a digestive fluid. After the insects are decomposed, the products are absorbed by the leaves. The pitchers of *Nepenthes* frequently collect so much clear water that it can be used by people for drinking. In such cases it would seem probable that the leaves not only furnish the plants with materials from the bodies of the captured insects but also with water.

The sundews (*Drosera* spp.) are small plants which have their leaves arranged in the form of a rosette (Fig. 75). These leaves are thickly covered with glands which are borne on slender stalks



FIG. 74. Pitcher leaf of *Nepenthes*. ( $\times \frac{1}{4}$ )

(Fig. 76). These glands excrete a sticky fluid in which insects become entangled when they come in contact with the leaf.



FIG. 75. *Drosera*, a carnivorous plant.  
( $\times \frac{1}{2}$ )

After an insect has been captured in this manner, the leaf incloses it while the glands excrete a fluid which digests the insect. The digested material is then absorbed by the leaf.

The Venus's-flytrap (*Dionaea muscipula*) is also a small rosette plant (Fig. 77). The petiole is expanded into a bladelike structure which serves for photosynthesis. The blade is specially fitted for capturing insects. It consists of two valves, each of which bears upon its upper surface three short, rather stiff bristles. Mechanical contact with these bristles causes

the two valves to close together. When an insect alights on the blade and brushes against these bristles, the leaf closes and



FIG. 76. Leaves of *Drosera*. (Redrawn after Darwin)

thus entraps the insect. The glands on the surface of the blade then excrete a fluid which digests the insect, after which the digested material is absorbed and the leaf opens.



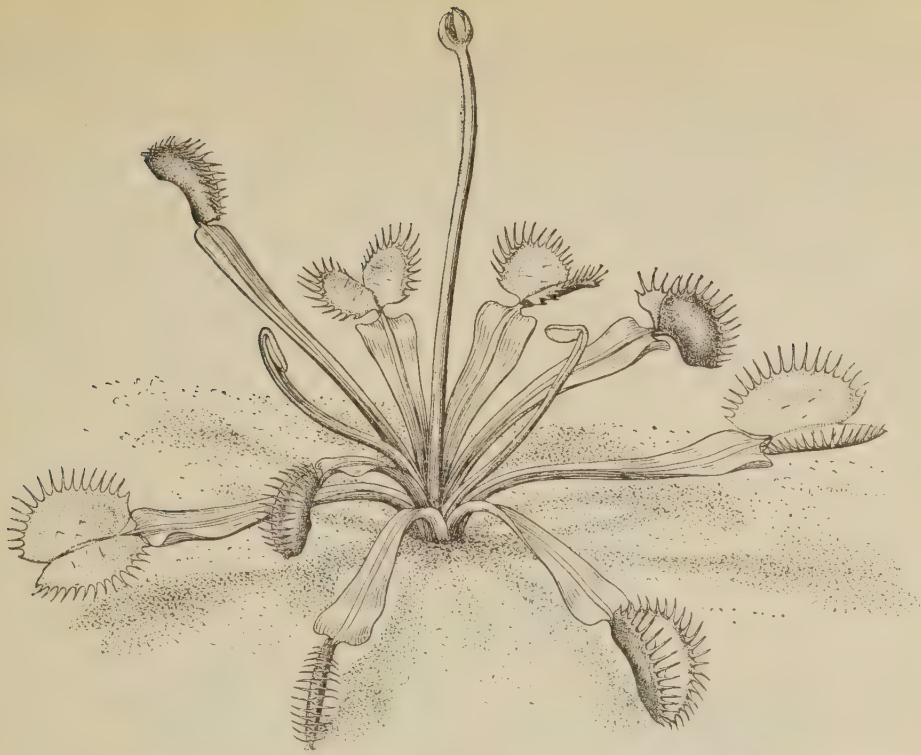


FIG. 77. Venus's-flytrap (*Dionaea muscipula*). ( $\times \frac{2}{5}$ )

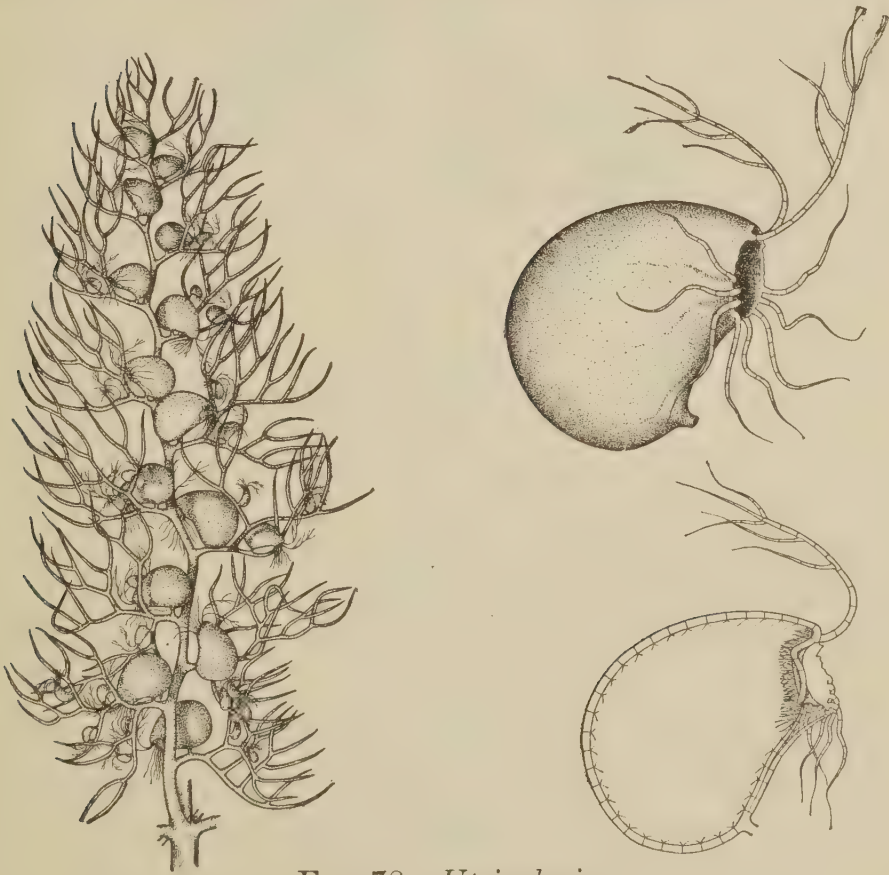


FIG. 78. *Utricularia*

Left, portion of a plant ( $\times 1$ ); upper right, an animal-catching bladder ( $\times 5$ );  
 lower right, section of animal-catching bladder ( $\times 5$ )

Plants of the genus *Utricularia*, some of which are submerged aquatics, are provided with bladders that entrap small animals in very much the same way as an ordinary trap catches a rat



FIG. 79. A *Utricularia* that lives on a very moist substratum

The horizontal stemlike structures are modified leaves which bear leaflike outgrowths and animal-catching bladders and function as roots. ( $\times 1$ )

water (Fig. 78), while others grow on a very moist substratum (Fig. 79). The latter have aërial shoots which bear flowers. In some forms there are ordinary leaves near the base of the plant, and also structures (Fig. 79) which are morphologically leaves but which have the appearance of horizontal branches and bear leaflike outgrowths and also animal-catching bladders. These

(Fig. 78). These bladders are provided with trap doors which allow the animals to enter and then bar their exit (Fig. 78). Small crustaceans may remain alive in these bladders for a considerable length of time, and it is probable that some of the products of their excreta are absorbed by the plant. They finally die and are decomposed by the action of bacteria. Nitrogenous products, which can be absorbed by the plants, are thus liberated.

Some species of *Utricularia* live in



branchlike leaves serve the purposes of roots, both in anchoring the plant and in absorbing water.

There are other forms of carnivorous plants, but those already mentioned will give some idea of the diversity of leaf structures used in capturing small animals.

Some carnivorous plants have properties which are usually regarded as characteristic of animals. The case of *Dionaea* is



FIG. 80. Branch of poinsettia (*Euphorbia pulcherrima*). ( $\times \frac{1}{4}$ )

particularly striking. This plant is able to respond to stimuli by movement, to excrete a digestive fluid and to digest animals, and then to absorb the products of digestion. Such cases serve to emphasize the fundamental similarity between animals and plants.

**Attraction of insects (floral function).** The principal function of white or brightly colored petals is to attract insects or other animals which pollinate the flowers. As we shall see later, the petals are modified leaves. Aside from petals there are other types of leaves which serve to attract insects. In some cases the flowers are small, and the function of attracting insects is performed by large white or brightly colored leaves. These leaves

may have the shape of ordinary foliage leaves and differ from them largely in being white or brightly colored, as in the case



FIG. 81. Bright-colored bracts surrounding the small flowers of *Bougainvillea spectabilis*. ( $\times \frac{1}{2}$ )

of the poinsettia (Fig. 80).

In other cases the leaves (bracts) have a shape very different from that of foliage leaves (Fig. 81). In many cases it is not the flowers themselves but the bracts that are showy.

**Reproduction (seed function).** Many plants can be propagated by means of leaf cuttings; this form of propagation is commonly practiced in the case of begonias. Some plants reproduce regularly in their wild state by means of leaves.

Striking examples are afforded by the so-called walking ferns and by *Bryophyllum*. The walking ferns have long leaves the tips of



FIG. 82. A walking fern (*Adiantum caudatum*). ( $\times \frac{1}{4}$ )

which reach the ground, strike root, and grow into new plants (Fig. 82). The leaves of *Bryophyllum* have small notches in their margins. When these leaves fall or are removed from the



parent plant, small plantlets grow from the notches (Fig. 83). These plantlets send roots into the soil and grow into large plants.



FIG. 83. Leaf of life plant (*Bryophyllum pinnatum*) producing small plants. ( $\times \frac{1}{3}$ )

**Storage.** Leaves that are specialized for storage can be divided into three general classes: leaves with special water-storage tissue, those with special food-storage tissue, and those forming pockets which collect materials from which the roots absorb such substances as are ordinarily obtained from the soil.

**Water storage.** Some plants which grow in very dry regions have leaves that are greatly thickened by water-storage tissue. Such tissue is very prominent in the leaves of the century plant (*Agave* spp.). Special water-storage tissue is not confined to leaves that are greatly thickened, but also occurs in some which have the appearance of ordinary foliage leaves (Figs. 45, 47). This is true of such plants as the India rubber tree (*Ficus elastica*).

**Food storage.** Fleshy bulbs are composed largely of thickened leaf bases, as in the onion (Fig. 84), or of whole leaves, as in lilies. In both cases the leafy part of the bulb serves for the storage of food.

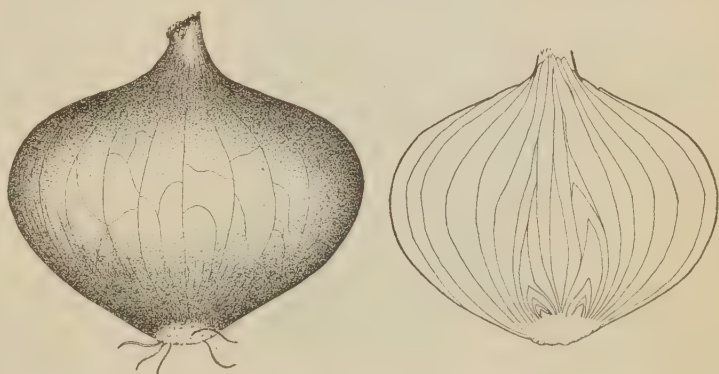


FIG. 84. Surface and sectional views of onion bulb formed of enlarged leaf bases. ( $\times \frac{2}{3}$ )

**Pocket leaves.** A considerable number of epiphytic tropical plants have the lower portion of their leaves, or special leaves, modified into pocket-like structures, in which leaves, dust, and other débris collect. The roots grow into this débris and absorb materials from it (Fig. 493).

The staghorn fern is a well-known example (Fig. 85). This plant has two types of leaves: ordinary foliage leaves which hang down, and collecting leaves which surround the mass of roots.



FIG. 85. A staghorn fern (*Platycerium bifforme*) growing on a coconut trunk. ( $\times \frac{1}{12}$ )

Water collects in the cups formed by the overlapping lower portions of the leaves of some bromeliads and is absorbed by the leaves (Fig. 490).

**Protection.** At the tip of a growing stem there is a soft, growing region which is surrounded and protected by the young leaves. This protection may be afforded by whole leaves or by stipules (Figs. 15, 86). Aside from this protective function many leaves are specially modified for protecting the plant. The different kinds of leaves which have this special function may be divided into

three classes: spiny leaves, motile leaves, and bud scales.

**Spiny leaves.** A large number of animals feed directly on plants. In some cases this is of advantage to the plants, as when birds eat the fruits of a plant and scatter the seeds; but the



feeding of animals on the foliage or stems can be regarded only as harmful to the plants. Many plants are protected from animals, to a greater or less degree, by the development of spines (Fig. 87). On the other hand, many spiny plants are eaten by browsing animals. Spines may be stem or root structures, but very frequently they are modified leaves. Whole leaves that are modified as spines (Fig. 44) may or may not serve for photosynthesis. The spines of the cacti are believed to be modified leaves (Fig. 512). In some cases spines are developed at the tip or on other portions of a leaf. The daggerlike leaf of the century plant is a striking example of a leaf whose tip is developed into a spine. Stipules are sometimes modified into stout spines (Fig. 88).

**Motile leaves.** The leaf bases of many leaves and the bases of the leaflets of many compound leaves are modified into motile organs known as *pulvini*. These are most conspicuous in compound leaves, where the whole leaf hangs down and the leaflets fold together at night (Fig. 89) or when exposed to intense sunlight. Such movements are the result of the bending of the pulvini. The significance of the drooping and folding up at night (sleep movements) is not understood, but it has been suggested that these movements serve to reduce the radiation of heat from the leaves. When leaves droop



FIG. 86. Stipules of India rubber tree (*Ficus elastica*)

The united stipules of the young opening leaf surround the bud, while those of the second leaf are about ready to fall. ( $\times \frac{1}{4}$ )

and fold up while exposed to intense sunlight, such movements seem to be fitted to reduce the rate of transpiration. The leaves of the sensitive plant (*Mimosa pudica*) not only show sleep movements but also fold up and hang down as a result of contact or of shaking (Fig. 90). When the plant is shaken, the leaflets of all the leaves may fold together and the pulvini of



FIG. 87. Marginal and stipular spines of the simple leaf of *Acanthus ilicifolius*. ( $\times \frac{1}{3}$ )



FIG. 88. Stipular spines of the bipinnate leaf of cassia flower (*Acacia farnesiana*). ( $\times \frac{1}{2}$ )

the leaves bend so that the leaves hang down. These movements result in a very striking change in the aspect of the plant. Instead of having a luxuriant display of foliage, it becomes very inconspicuous. The significance of these movements is not clear, but they would seem to afford some protection from browsing animals.

**Bud scales.** We have seen that the tips of stems are protected by leaves. We also find that many deciduous plants have specially modified leaf structures which protect the buds during the season in which the tree is leafless (Fig. 94). These structures are known as bud scales and may represent whole leaves, petioles with undeveloped blades, or stipules. Bud scales





FIG. 89. Day and night positions of a leaf of a rain tree (*Enterolobium saman*). ( $\times \frac{1}{3}$ )



FIG. 90. Leaves of sensitive plant (*Mimosa pudica*) before and after stimulation. ( $\times \frac{1}{3}$ )

are frequently covered with gummy or resinous substances and afford excellent protection to the bud.

The bracts which cover some types of unopened flowers are also modified leaves which have a protective function.

In this category we may also include the reduced leaves of parasitic and saprophytic plants. Such plants do not produce chlorophyll, and have only small reduced leaves whose only function would seem to be that of protecting the buds.



## CHAPTER V

### THE STEM

The chief function of the stem is to support the leaves and reproductive organs in such a manner that they can advantageously carry on their several functions. When we analyze this function of the stem, we find that several aspects must be considered. These can be grouped under attachment, position, and increase in number of leaves and reproductive organs.

**Attachment.** The stem furnishes any organ which it bears with a place of attachment, and thus enables that organ to maintain its position.

**Position.** In most cases, stems serve to distribute the leaves in such a manner that they do not shade each other to any great extent. Insect-pollinated flowers are usually in such a position that they are readily visible to the pollinating agents, while wind-pollinated flowers are so exposed that the pollen may be carried by wind from one flower to another. Stems support most fruits in such a way that they may be readily distributed by disseminating agents.

**Increase in number.** Many stems serve greatly to increase the number of leaves and reproductive organs that are produced by the plant. The stem, by increasing the number of leaves that the plant bears, enables the plant to produce more food and, consequently, a greater number of seeds.

**Incidental functions.** Besides the main function of support the stem has two important incidental functions: namely, to conduct water from the roots to the leaves and reproductive structures, and to carry food from the leaves to other parts of the plant. It is evident that if leaves and flowers were attached directly to the roots, there would be no need and no possibility for any other organ to conduct materials between roots and leaves.

The stem is frequently an important storage organ. During a large part of their lives many plants manufacture food faster than it is used; in most cases a large part of this surplus is stored in the stem. A stem is a better storage organ than an ordinary leaf, as it is usually a more permanent structure. Moreover, it is of advantage to the plant that the surplus food manufactured in the leaves is removed from them, so that food material does not accumulate and interfere with its continued production.

### STRUCTURE OF STEMS

**Nodes and internodes.** The stem (Fig. 91) is composed of *nodes* (the places where leaves and branches originate) and *internodes* (the parts of the stem between the nodes). Branches usually



FIG. 91. Horizontal branch of guava (*Psidium guajava*). ( $\times \frac{1}{3}$ )

originate at the nodes in the axils of the leaves, that is, just above the point of attachment of the leaves.

#### Apical growth.

The growth in length of a stem takes place largely, and in most cases only, at and near

the tip. Very good evidence of this fact is afforded by an examination of an actively growing stem of a dicotyledonous plant (Fig. 91). It will be seen that all the leaves, except those near the tip, are of about the same size, and that the internodes are of approximately equal length. The similarity in size of the leaves shows that no new leaves are formed on the older parts of the stem, while the similarity in length of the internodes proves that when an internode has reached a certain length, elongation ceases. If all parts of the stem were to continue to grow in length throughout their existence, the internodes would



be progressively longer toward the base of the stem. Near the tip of a growing stem (Figs. 15, 91) the leaves are very minute, while toward the lower part of the stem they are progressively larger until they reach mature size. The internodes near the tip are also very short, but away from the tip they become progressively longer until they also assume a definite length. The explanation of this is that new leaves and internodes are formed



FIG. 92. Section through apex of the stem of a water plant  
Left, through whole bud ( $\times 60$ ); right, through apex only ( $\times 400$ )

at the tip, and that they soon reach their mature length and then show no further growth in length. Growth at the tip of an organ is called *apical* growth.

The apical growth of a stem is due to the activity of a few actively dividing cells which are found at the very tip of the stem. This part of the stem is hidden by the young leaves produced near the tip, and cannot be seen until these leaves are removed (Fig. 92). A group of actively dividing cells is called *meristem*.

**Intercalary growth.** In addition to apical growth some plants have another type of growth known as intercalary growth. This type of growth is very prominent in the stems of grasses. In

grasses a group of cells just above each node remains meristematic for a considerable period of time and by division forms new cells, thus increasing the length of the internode. When the growing stem of a grass is pulled apart, it will usually break just above a node, where the soft meristematic tissue is located. This meristematic tissue in the grasses does not usually have



FIG. 93. Buds in the axils of leaves of mulberry (*Morus alba*)

The dots on the stem are lenticels. ( $\times \frac{3}{4}$ )

enough strength to support the stem but is reënforced by the sheathing leaf bases (Fig. 68). This is evident when these leaf bases are removed, as the young stem will bend in the region of meristematic tissue. Even where intercalary growth is found it is not so important as apical growth, for apical growth produces new nodes and internodes, while intercalary growth only increases the length of the nodes to a limited extent.

**Position of leaves.** Leaves are formed only at the tip of a stem. They grow to mature size, perform their functions for a time, and finally fall from the stem. As no new leaves are formed on the older parts of a stem, the old portions of branches are always leafless, the leaves being confined to the smaller and younger portions. When leaves appear, on superficial observation, to arise directly from large trunks or branches, they really occur on short branches that are too small to be conspicuous.

**Leaf scars.** When leaves fall, they leave scars, known as leaf scars (Fig. 94), on the stem. These scars persist for a considerable length of time and mark the location of the nodes long after the leaves have fallen. In each scar are a number of more or less conspicuous dots, which in each species are arranged in a definite pattern. These dots mark the places where groups of xylem and phloëm cells (called vascular bundles) passed from the stem to the leaf.



**Buds.** On stems that normally branch, buds are usually produced in the axils of all the leaves (Fig. 93). Buds are also found at the tips of stems, unless the bud has died or produced a terminal flower or flower cluster which has dropped off and ended the longitudinal growth of the stem. When the life of a terminal bud is ended by the production of a flower cluster, the continued growth of the shoot is due to one or more axillary buds. Buds are undeveloped shoots. After they are formed, they may either develop into shoots or remain dormant. A bud that has been dormant for a number of years may be forced to develop into a shoot by the removal of that part of the stem which is above the bud.

**Bud scales.** Buds are protected by a covering of leaves. When deciduous trees are leafless for a considerable period, the dormant buds found on them during that time are usually covered by specially modified protecting leaves known as bud scales (Fig. 94). These are



FIG. 94. Leafless branches of elm (left) and horse-chestnut (right), with winter buds protected by bud scales

The main branch of the elm has three rings of bud-scale scars, showing that the lower part of the branch is four years old. A ring of scars at the base of each side branch shows that these branches are the previous summer's growth ( $\times \frac{1}{3}$ ). The branch of horse-chestnut also has three rings of scars, showing that the lower part of the branch is four years old ( $\times \frac{1}{3}$ )



FIG. 95. A branch of the *Erythrina indica*, a tropical tree which is leafless during the dry season

This branch is marked by three rings of scars left by the falling of scales which protected the bud during successive dry seasons. The three rings show that the lower part of the branch is four years old. ( $\times \frac{1}{4}$ )

in the formation of rings of bud-scale scars may be connected with either a long cold season or a severe dry season (Fig. 95). Trees which do not shed their leaves may have their branches marked by

described in the preceding chapter. When bud scales fall, they leave scars, just as do ordinary leaves. Usually, however, the scars of bud scales are considerably smaller and much more crowded together than are those of ordinary leaves. The result is that when the scales around a dormant bud fall, the crowded bud-scale scars frequently form a conspicuous ring around the stem and thus enable us to determine much of the history of that stem. A season's growth always begins just above a ring of bud-scale scars and ends with the formation of a new set of scales,

so that by counting the rings of bud-scale scars we can tell the age of a branch. Also, by examination of the part of the stem between the rings we can tell how much growth was made during past seasons and the number of leaves borne by the branch during those seasons. The falling of leaves which results in leafless branches and also



FIG. 96. Opposite leaves on an upright branch of guava (*Psidium guajava*) Compare position of leaves in Fig. 91. ( $\times \frac{1}{4}$ )



rings of bud-scale scars if growth in length is seasonal and the buds are protected by scales.

When stems continue to grow and bear leaves throughout the year, there are of course no rings of bud-scale scars, and it is not possible to tell the age of a branch by inspection.

**Lenticels.** The epidermis of the very young parts of a stem contains stomata. As the stem grows older these are replaced by lenticels, which are groups of loosely arranged cells that allow an exchange of gases between the interior of the stem and the external atmosphere. On the younger internodes these can usually be seen as brownish spots with raised borders (Fig. 93).

**Arrangement of leaves.** The leaves occur on the stem in a number of dif-

FIG. 97. Diagram showing the arrangement of two-ranked leaves

ferent arrangements. The system of leaf arrangement is known as *phyllotaxy*. When two leaves are attached opposite each other at the node, they are called *opposite* leaves (Fig. 96). On vertical stems each pair of opposite leaves is borne at right angles to the point of attachment of the pairs above and below it, so that the attachment of the leaves occurs on the stem in four vertical rows, or ranks (Fig. 96). When three or more leaves are attached to the same node, they are designated as *whorled*. Whorled leaves are attached above and below points between the points of attachment of the leaves of neighboring whorls, except when there

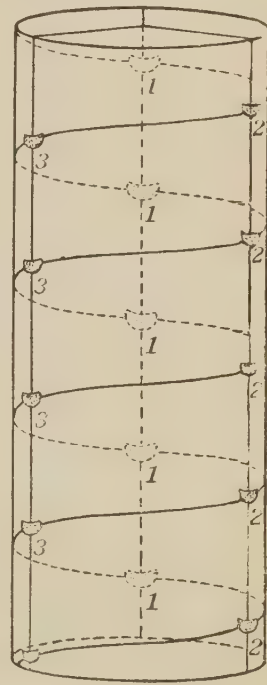
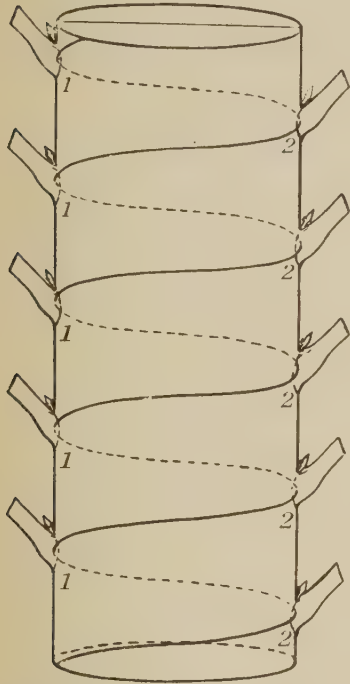


FIG. 98. Diagram showing the arrangement of three-ranked leaves

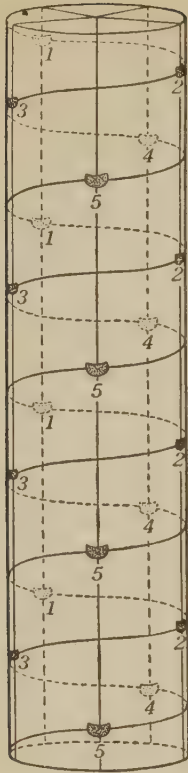


FIG. 99. Diagram showing the arrangement of five-ranked leaves

In this diagram the top of the cylinder is divided into five equal sectors, while from the end of each dividing line runs a line down the stem through a row of leaves, showing that the leaves are in five rows. The five vertical lines divide the stem into five equal parts, so that the distance around the stem that one leaf is from the next in age (as from leaf 2 to leaf 3) can be determined. This distance is two fifths of the circumference, so that the divergence is  $2/5$ . Between two consecutive leaves in the same vertical row there are two turns of the spiral

are irregularities in the whorls. If only one leaf occurs at a node, the leaves are said to be *alternate* (Fig. 110). Alternate leaves are arranged in a spiral around the stems, and the leaves have a definite location in the spiral. This location varies with different species.

**Phyllotaxy of alternate leaves.** In some cases alternate leaves occur only on two sides of the stem, so that every leaf is above the second one below (Fig. 68). Such leaves are in two rows (two-ranked), and each leaf is halfway around the stem from the next in age (Fig. 97).

Another arrangement is in three ranks, in which the point of attachment of every leaf is directly above that of the third leaf below (Fig. 98) and there is a complete turn of the spiral for every three leaves. If we include the leaf which begins a turn of a spiral and also the one which ends it, there are, of course, four leaves; but when we take into consideration the whole length of the stem, there will be noted a turn for every three leaves.

The commonest arrangement is in five ranks, with the point of attachment of each leaf  $2/5$  of the way around the stem from that of the leaf next in age (Figs. 99, 110). In such arrangement the point of attachment of every leaf is directly above that of the fifth leaf below, and there are two turns in the spiral for every five leaves.

Still another method of arrangement is in eight ranks, with the point of



attachment of every leaf  $\frac{3}{8}$  of the way around the stem from the next in age (Fig. 100). In this case the point of attachment of a leaf is directly above that of the eighth below, and there are three turns in the spiral for every eight leaves.

**Divergence of alternate leaves.** The proportion of the distance around the stem that a leaf is removed from the one next in age is called the *divergence*. When leaves are two-ranked (halfway around the stem from each other) the divergence is  $\frac{1}{2}$ . We have just considered cases in which the divergence is  $\frac{1}{2}$ ,  $\frac{1}{3}$ ,  $\frac{2}{5}$ , and  $\frac{3}{8}$ . These figures, however, show other relations than the divergence. In the case of a divergence of  $\frac{3}{8}$  (Fig. 100) the denominator 8 shows the number of internodes between two successive leaves that are in the same vertical line on the stem, and also the number of vertical rows in which the leaves are arranged on the stem. The numerator 3 shows the number of turns of the spiral for every eight leaves. The same relation holds for all other divergences. In the case of  $\frac{2}{5}$  the denominator 5 shows the number of internodes between two successive leaves that are on the same vertical line and the number of rows in which the leaves are arranged. The numerator 2 shows that there are two turns in the spiral for every five leaves. When the divergence is  $\frac{1}{3}$ , every leaf is above the third below, the leaves are arranged in three rows, and there is one turn of the spiral for every three leaves.

The greatest divergence that occurs with alternate leaves is  $\frac{1}{2}$ , and the smallest is  $\frac{1}{3}$ . All other divergences are intermediate between these two.

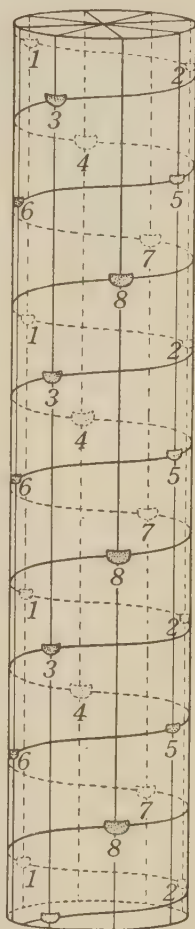


FIG. 100. Diagram showing arrangement of eight-ranked leaves

**Series of divergences.** The divergences for alternate leaves can be arranged in the following series:  $1/2$ ,  $1/3$ ,  $2/5$ ,  $3/8$ ,  $5/13$ ,  $8/21$ ,  $13/34$ ,  $21/55$ , etc. Each fraction represents the part of the way around the stem that one leaf is from the next in age. In each fraction the denominator represents the number of

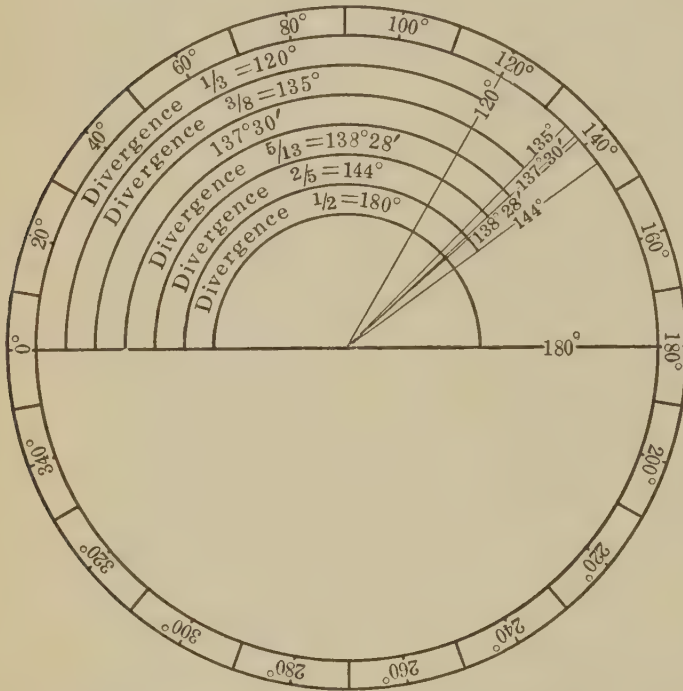


FIG. 101. Diagram showing the divergence of alternate leaves, expressed in degrees of circumference

All divergences lie between  $1/3 = 120^\circ$  and  $1/2 = 180^\circ$ , while all members of the series higher than  $2/5$  lie between  $2/5 = 144^\circ$  and  $3/8 = 135^\circ$ . The members higher than  $5/13$  lie so close to the theoretical limit of  $137^\circ 30'$  that it is not practicable to show them on a diagram of this size

leaves; the second figure,  $1/3$ , is the smallest; the third figure,  $2/5$ , is the second largest; the fourth figure,  $3/8$ , is the second smallest; the fifth figure,  $5/13$ , is the third largest; the sixth figure,  $8/21$ , is the third smallest; the seventh figure,  $13/34$ , is the fourth largest; and the eighth figure,  $21/55$ , is the fourth smallest, etc. This can be expressed in a different way. If we take the first figure in the series and then every second figure, we obtain the following descending series of divergences:  $1/2$ ,

internodes between successive leaves that are situated in the same vertical row, and also the number of vertical rows of leaves on the stem, while the numerator shows the number of turns of the spiral between two successive leaves in the same vertical row. It should be noted that the numerator and denominator for every divergence can be obtained by adding together those of the two preceding fractions in the series.

The first figure in the series,  $1/2$ , is the greatest divergence that occurs with alternate



$2/5$ ,  $5/13$ ,  $13/34$ . If we take the second figure in the series and then every other figure, we obtain the following ascending series of divergences:  $1/3$ ,  $3/8$ ,  $8/21$ ,  $21/55$ . The divergences of these series expressed in degrees and minutes of circumference can be tabulated as follows:

$1/2 = 180^\circ$	$1/3 = 120^\circ$
$2/5 = 144^\circ$	$3/8 = 135^\circ$
$5/13 = 138^\circ 28'$	$8/21 = 137^\circ 8'$
$13/34 = 137^\circ 39'$	$21/55 = 137^\circ 27'$

The largest figure in the ascending series is never as large as the smallest in the descending series, and both series approach the same limit, which is

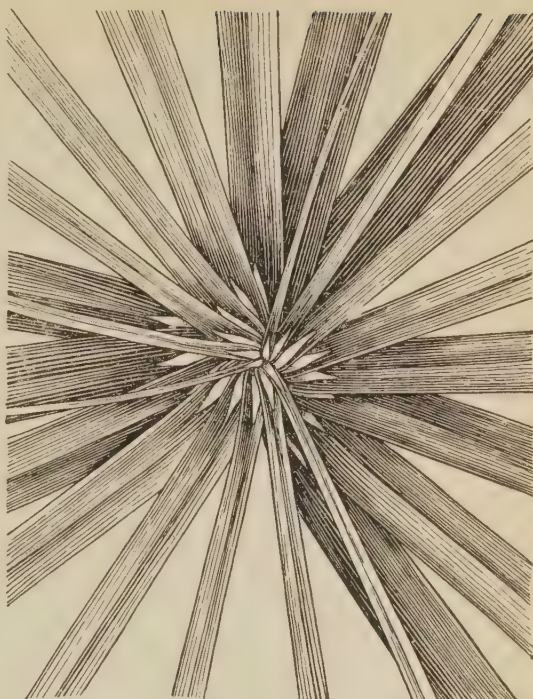


FIG. 102. Top view of a stem of the umbrella plant (*Cyperus flabelliformis*), showing three-ranked leaves on a twisted stem

The three rows of leaves can be traced by means of the axillary buds. ( $\times \frac{1}{3}$ )



FIG. 103. Coconut palms along a seacoast



a divergence of  $137^{\circ} 30' 28''$ . The above figures for the ascending and descending series show that all members of the original series have values which lie within the limits  $1/2$  and  $1/3$ . Likewise, the values for higher members than  $3/8$  lie between  $2/5$  and  $3/8$ , and the values for higher members than  $8/21$  lie between  $5/13$  and  $8/21$ . The difference between the divergences  $13/34$

and  $21/55$  is only  $12'$ , or  $1/5$  of a degree, and the difference between all higher members of the series must be less than this. There is, therefore, very little difference between the divergences of the higher members of the series. This relationship is shown in Fig. 101.



FIG. 104. Excurrent crown of *Casuarina*

The phyllotaxy is frequently obscured by a twisting of the stem. A very striking case is that of the umbrella plant. Here the leaves are in three rows, but the stem is so twisted that the leaves radiate in all directions (Fig. 102).

**Branching.** Many stems branch and thereby increase the number of leaves and flowers which they can advantageously support. Since buds grow in the axils of the leaves, the arrangement of the branches would be the same as that of the leaves if all buds produced branches. Usually, however, many of the buds fail to grow. Some plants, as is the case with numerous palms (Fig. 103), do not branch at all. In many species the main stem continues to grow throughout the life of the plant and is very much more vigorous than any of the branches (Fig. 104). Plants that have



this form of growth are said to be *excurrent*. In trees with excurrent growth the main trunk extends as a central shaft to the top of the tree, while the branches spread from it more or less horizontally. This results in a conical crown. The opposite form of growth is known as *deliquescent* (Fig. 105). In trees that have this form the main trunk is short, while the branches divide into smaller and smaller branches, producing a spreading crown.

**Adventitious buds.** Most branches originate from buds in the axils of the leaves and are called axillary branches. Buds may, however, arise from the internodes, the roots, or even the leaves (Figs. 82, 83), especially as the result of injury. Such buds are said to be adventitious buds, and branches produced by them are adventitious branches. The growth of adventitious buds is made use of in the process of pollarding, that is, the cutting back of the tree to the trunk to promote a dense growth of branches which arise from the tissue produced around the wound. In the case of the willow, pollarding produces slender branches, which are used in making baskets. In propagation by root cuttings, which is practiced in some species, advantage is taken of the fact that some roots produce adventitious buds.



FIG. 105. Deliquescent crown of a rain tree  
(*Enterolobium saman*)

is made use of in the process of pollarding, that is, the cutting back of the tree to the trunk to promote a dense growth of branches which arise from the tissue produced around the wound. In the case of the willow, pollarding produces slender branches, which are used in making baskets. In propagation by root cuttings, which is practiced in some species, advantage is taken of the fact that some roots produce adventitious buds.

#### RESPONSE OF STEMS AND LEAVES TO EXTERNAL CONDITIONS

**Geotropism.** It is a very common observation that stems grow upward and roots downward. Even in the case of most prostrate stems the tips tend to grow upward. This tendency of stems to grow upward and roots to grow downward is due to

the force of gravity. Such responses of a plant to gravity are known as geotropism. When roots grow downward, or in the direction of the force of gravity, they are said to show *positive geotropism*, while stems that grow upward against the force of gravity exhibit *negative geotropism*.

The action of geotropism can be demonstrated very easily if we take a small seedling and lay it in a horizontal position.



FIG. 106. The tip of a pendent stem of an orchid (*Dendrobium anosmum*) (see Fig. 2) producing a young plant

The parent plant hangs under the edge of a porch; the new shoots are growing toward the light, and the roots away from the light. ( $\times \frac{1}{4}$ )

The stem will bend upward, while the root will turn downward. The stem and root will then continue to grow in these directions. If, however, we place a seedling in a horizontal position and revolve it around its own axis, so that all sides will be subjected in the same way to the force of gravity, then the stem and root will continue to grow in a horizontal direction.

The action of the negative geotropism of stems is clearly seen in the case of plants which have been blown over but continue to grow. In such cases the stems grow upward, away from the surface of the earth.

The action of geotropism is not due to a direct pull of gravity on the plant but is a response of the plant itself, as is shown by the fact that stems grow upward against the pull of gravity, while roots may exert considerable force in growing downward; in fact, roots must exert force to penetrate the ground. The difference in reaction of stems and roots is not the result of any difference in the force of gravity on the parts concerned



but is caused by differences inherent in the organs themselves. The response to gravity is brought about by different rates of growth on the upper and lower sides of the organs concerned, the side which becomes convex growing more rapidly than the opposite side. Geotropism is largely responsible for the position of upright stems. Branches do not show the action of geotropism to the same extent as does the main axis.

**Phototropism.** Stems tend to grow toward the light, while most aërial roots grow away from the light (Fig. 106). The tendency of plant organs to orient themselves with reference to light is called phototropism. An organ that grows toward the light exhibits *positive phototropism*, while an organ that grows away from the light shows *negative phototropism*. Nearly all roots that normally grow in the ground show little or no phototropism;



FIG. 107. A radish seedling grown on the side of a piece of blotting paper held vertically in a darkened box with light entering on the left side

The position of the shoot is due to a combination of positive phototropism and negative geotropism; that of the root, to negative phototropism and positive geotropism. ( $\times 1$ )

but there are some exceptions, as in the case of the radish, where the roots are negatively phototropic (Fig. 107).

The effect of phototropism can often be clearly seen in upright plants growing very near a house. In such cases there is a tendency for the branches to grow away from the house, or, in other words, toward the source of greatest illumination. There is also a tendency for the main stem to lean away from the house, or toward the light. In trees that bend toward the light the position of the main axis is very clearly the result of the combined action of geotropism and phototropism. The general upright position of the stem is due to geotropism, while the leaning position is the result of phototropism. The effects



FIG. 108. A mungo bean seedling which grew upright when illuminated from all sides and then bent toward the light when illuminated only from the left. ( $\times \frac{1}{2}$ )

leaves above them. The turning and bending of leaves to face the light is called diaphototropism.

When leaves have petioles, the bending takes place in the petioles. If the petioles on pendent branches were straight, the morphologically upper side of the leaves would face downward, but in such cases the petioles bend and twist so as to expose this side to the strongest light (Fig. 109).

of phototropism are frequently pronounced in plants growing in windows or on covered porches. In such cases the plants usually lean toward the source of light (Fig. 108).

The tips of herbaceous stems frequently follow the course of the sun during the day, pointing to the east in the morning and to the west in the afternoon. This is true of the sunflower.

**Diaphototropism.** Leaves usually turn to face the source of greatest illumination, and also bend in such a way that they are not greatly shaded by the



FIG. 109. Leaves of *Thunbergia grandiflora* on pendent branch

The petioles have twisted so that the morphologically upper sides of the leaves are uppermost. ( $\times \frac{1}{4}$ )



In many cases the bending and twisting of the petioles or the twisting of the stem is much more important than the place of attachment of the leaves in determining the position of the leaf blades. This is often very clearly seen in the different positions of leaves

on vertical and horizontal stems of the same plant. On vertical stems, which are not shaded on one side, the leaves extend straight out from the point of attachment, while if the illumination is one-sided, as upon unshaded horizontal branches, the stems or petioles frequently bend and twist so as to bring the blades into such a position that they face the strongest light.

Compare Fig. 91 with Fig. 96, and Fig. 111 with Fig. 110. On horizontal branches the leaves are often

arranged in an approximately horizontal position. As an example take the case of a plant on which the leaves are arranged in five vertical rows. On a vertical stem the leaves will extend from the stem in five directions (Fig. 110). On a horizontal branch of the same plant the petioles will bend and twist so as to bring the blades into an approximately horizontal position, and the leaves will appear to grow from only two sides of the stem (Fig. 111).



FIG. 110. Vertical branch of *Cestrum nocturnum* illuminated from all sides

Compare with Fig. 111. ( $\times \frac{1}{3}$ )

The degree of adjustment of leaves in response to light varies greatly in different plants. Leaves which are very sensitive to light follow the course of the sun during the day; leaves which are only moderately sensitive usually face the strongest light, as is the case with most common trees and shrubs; while leaves which are feebly sensitive are not so definitely arranged.

**Unusual positions of leaves.** While the leaves of most plants are in general arranged so that they face the source of greatest illumination, there are some exceptions. The leaves of many



FIG. 111. Arrangement of leaves on horizontal branch of *Cestrum nocturnum*; position of leaves due to one-sided illumination

Compare with Fig. 110. ( $\times \frac{1}{3}$ )

plants, particularly of those growing in arid regions, make acute angles with the rays of light from the source of greatest illumination. This arrangement has certain advantages. Very intense light has a tendency to destroy chlorophyll. It also has a tendency to heat the leaves excessively and to produce rapid tran-

spiration. These injurious effects are partly avoided by plants that have their leaves arranged in the manner just described.

**Leaf mosaics.** The petioles of old leaves are usually longer than those of younger leaves on the same branch. In many plants the bending and twisting of the petioles, or a combination of these movements with different lengths of the petioles, brings all the blades into approximately the same plane and in such a position that they fit in between each other with very little overlapping. Such an arrangement of the blades is called a leaf mosaic, from the similarity to the fitting in of materials in mosaic work.

**Heliotropism.** The term *heliotropism* is often used in place of the word *phototropism*. Heliotropism is the orientation of plant



organs in response to sunlight. Stems and leaves, however, respond to artificial light as well as to sunlight, so that it is better to use the general term, *phototropism*, than the specific one, *heliotropism*.

**Etiolation.** Stems that grow in the dark have a tendency to grow longer and to be more slender than those that develop in the light. They also have a blanched appearance, due to a lack of

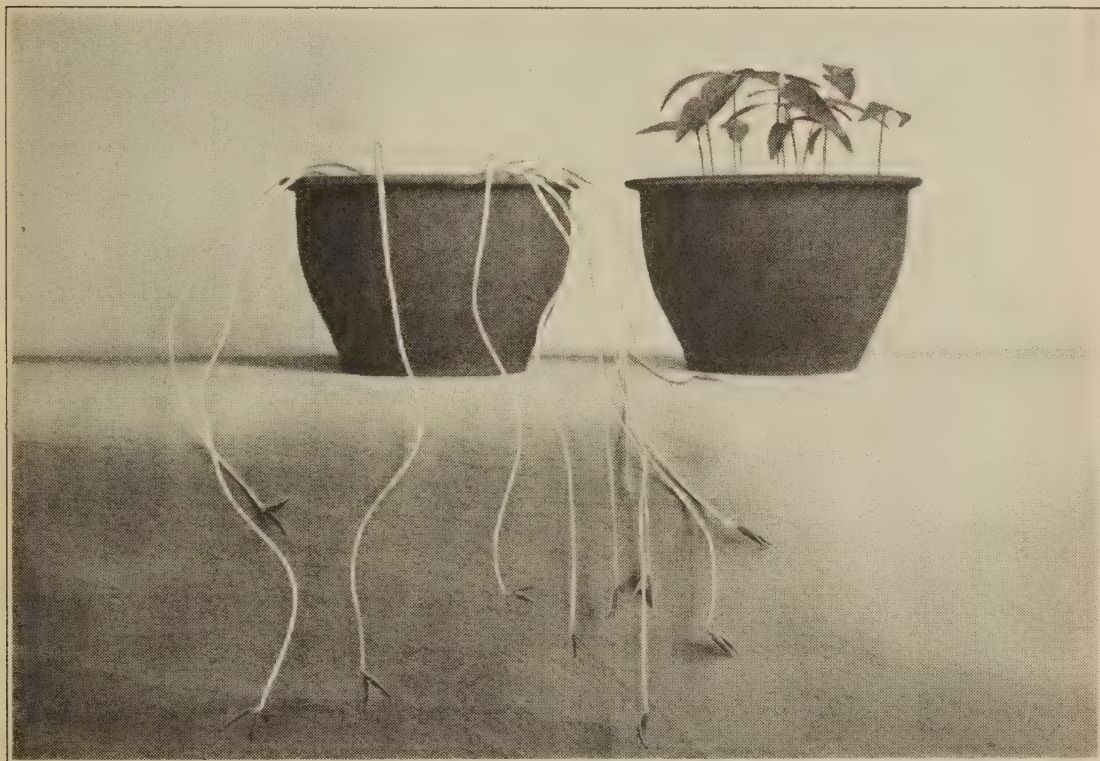


FIG. 112. Etiolated seedlings (left) and normal seedlings (right) of mungo bean (*Phaseolus radiatus*)

chlorophyll. The leaves of plants grown in the dark are usually small and also have a blanched appearance. Plants that have stems and leaves with these characteristics, which are the result of growth in the dark, are said to be etiolated. Etiolation is well illustrated in Fig. 112. A practical use is made of etiolation in China and Japan, where young sprouts of bamboo are used for food. These are made white and tender by covering them with earth or earthenware jars. Similar results are achieved with asparagus by cutting the shoots when the tops are just aboveground.

In nature, when upright stems grow in the dark, they usually arise from underground structures such as bulbs or rhizomes, or are produced by germinating seeds. In such cases the relatively longer, slender structure of etiolated stems has a tendency to make the plants reach up into the light. The production of small leaves on etiolated stems also seems to be of advantage, as leaves in the dark cannot carry on photosynthesis and so are of no particular use to the plant. Moreover, large leaves would hinder the growth of stems through the ground, while their formation would require material which could be used in elongating the stem.

Leaves that normally arise directly from underground structures behave differently from ordinary aërial leaves when grown in the dark. Instead of being smaller than usual they become longer. This has the same effect as the elongated growth of upright stems in that there is a tendency to bring the leaves into the light.

**Self-pruning.** The heavily shaded portions of branches frequently shed their leaves, while whole branches that are heavily shaded usually die and fall from the plant. It is for this reason that the leaves of trees are usually found near the circumference of the crown and not in the interior.

The loss of shaded branches can be seen very plainly in the case of trees which grow close together and produce long trunks. As the lower branches become heavily shaded they die and fall from the tree, and leave the lower part of the trunk clear of branches. It is a common observation that trees growing close together are tall and slender in form and have long, clear trunks, while a tree growing in the open, where it is not shaded, usually has a spreading crown and a short trunk. These differences are due to the fact that if trees grow close together the lower portions are shaded and the lower branches die, which is not the case with trees which develop in the open. The dying and falling of shaded branches is called self-pruning. Foresters take advantage of the self-pruning of trees, and plant seedlings close together so that long, clear trunks will be produced. If it is desired that a tree growing in the open shall have a long, clear trunk, it frequently becomes necessary to remove the lower branches.



## THE TWO TYPES OF STEMS

Flowering plants, as previously noted, are divided into two general classes, *monocotyledons* and *dicotyledons*. Monocotyledons are plants that have one cotyledon, or seed leaf, and dicotyledons those that have two cotyledons. The *cotyledons* are the first leaves produced by plants and are usually found in the seed. When there are two, they are opposite each other, but plants with two seed leaves frequently do not have their subsequent leaves opposite each other. The leaves of dicotyledons have netted veins (Fig. 16), while those of monocotyledons usually have parallel veins (Fig. 16). If a dicotyledon reaches any considerable size, it has a bark which can be readily stripped from the remainder of the stem, while monocotyledons do not have bark. Stems of monocotyledons reach a certain diameter and then do not usually become thicker, while stems of dicotyledons generally continue to grow in thickness as long as the plant lives. The floral parts of monocotyledonous plants are usually arranged in threes or in multiples of three, while in dicotyledonous plants the numbers vary, but they rarely occur in threes or multiples of three. The most important monocotyledons are grasses, including bamboos, sugar cane, and all cereals such as corn, rice, and wheat; sedges (plants which resemble the grasses in appearance); palms (Fig. 103); members of the lily family and related families; orchids; aroids; and members of the ginger (Fig. 172) and banana (Fig. 66) families. Dicotyledonous plants are much more numerous and include all ordinary trees, shrubs, and many small plants. The structure of the stem of a monocotyledonous plant is, as we shall see, very different from that of a dicotyledonous plant.

## ANATOMY OF DICOTYLEDONOUS STEMS

**General regions.** In young dicotyledonous stems there are three distinct regions (Fig. 113). The outermost is the *epidermis*. Within the epidermis there is a zone that has the shape of a hollow cylinder and is known as the *cortex*. The center of the stem is occupied by a solid column, the *stele*.

**Epidermis.** The epidermis of the stem resembles that of the leaf very closely in both structure and function. It consists of a single layer of cells and is the outermost layer of the stem. It contains stomata and produces various types of trichomes.

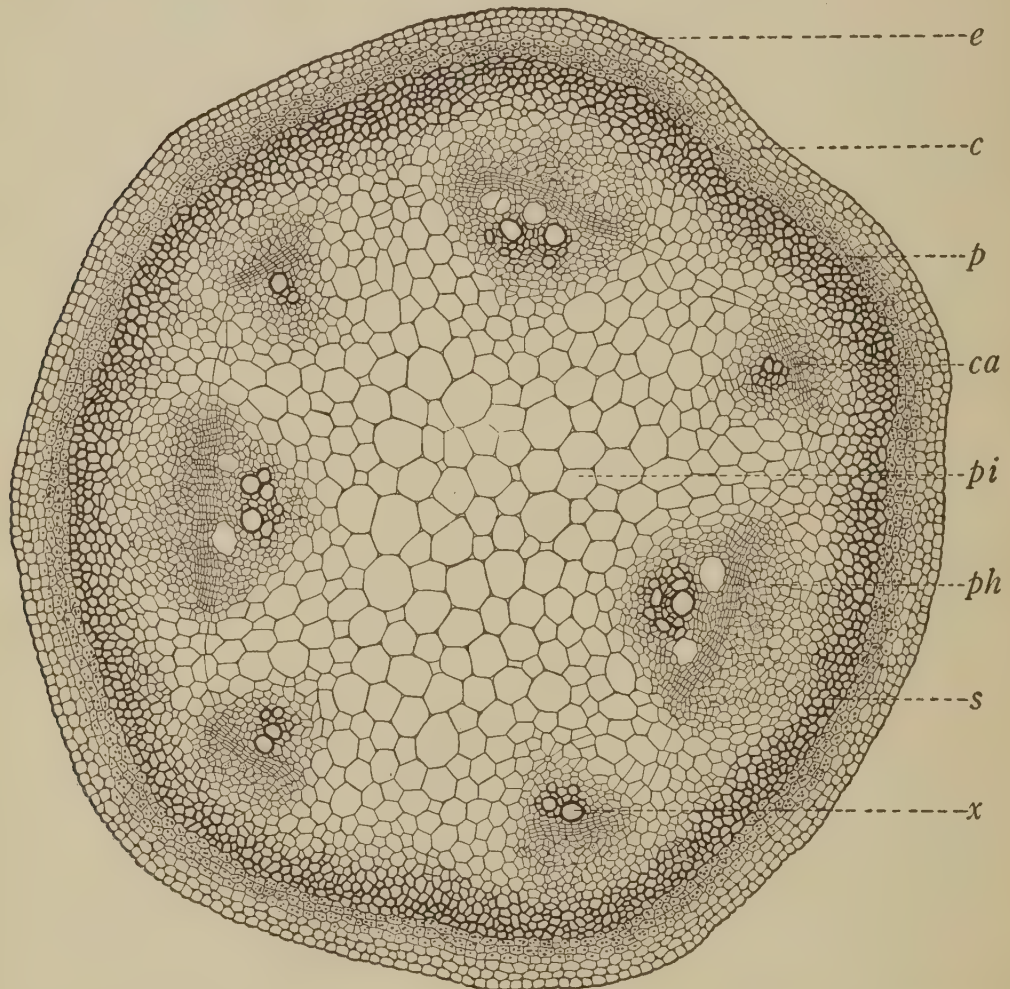


FIG. 113. Cross section of a young stem of *Aristolochia elegans*  
*e*, epidermis; *c*, collenchyma of cortex; *p*, parenchyma; *ca*, cambium; *pi*, pith ray;  
*ph*, phloem; *s*, sclerenchyma of pericycle; *x*, xylem. ( $\times 55$ )

The outer cell walls are greatly thickened and heavily cutinized (Figs. 115, 116). The epidermis serves chiefly for restricting the rate of transpiration and for protecting the underlying tissues from mechanical injury and from disease-producing organisms.

**Cortex.** The region that lies next to the epidermis is the cortex. The innermost layer of the cortex is the *starch sheath*, known also as the endodermis. It consists of a single layer of



cells which surrounds the stele and contains numerous starch grains, from which circumstance its name is derived (Figs. 114, 116). Frequently it is most easily distinguishable from the surrounding tissue by the presence of these starch grains. The part of the cortex situated between the epidermis and the starch sheath is usually divided into two regions, an inner zone of parenchyma and an outer zone of collenchyma cells (Figs. 113-115).

**Parenchyma.** The parenchyma cells of the cortex have the general structure and functions characteristic of parenchymatous cells (Figs. 113-115). Such cells are not highly specialized in structure for the performance of any particular function, but may be regarded as generalized cells which carry on to a limited extent all the usual functions of cells.

Parenchyma cells are ordinarily regular in shape, have comparatively thin walls, and are not greatly elongated in any

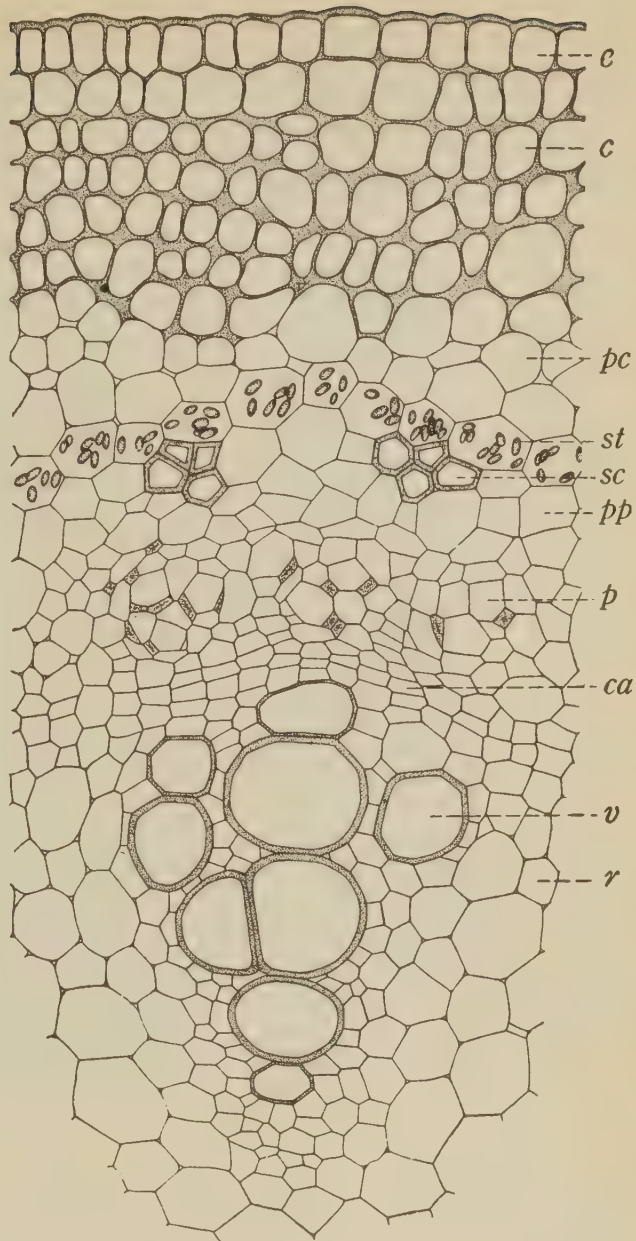


FIG. 114. Cross section of a portion of stem of castor-oil plant (*Ricinus communis*), showing a vascular bundle and the tissues around and external to it

*e*, epidermis; *c*, collenchyma; *pc*, parenchyma of cortex; *st*, starch sheath; *sc*, sclerenchyma of pericycle; *pp*, parenchyma of pericycle; *p*, phloem; *ca*, cambium; *v*, xylem vessel; *r*, pith ray. ( $\times 180$ )

direction. They are living cells and contain a moderate amount of protoplasm. When they are exposed to the light they develop chloroplastids and are known as chlorenchyma cells. Chlorenchyma cells are thus only a special kind of parenchyma cells.

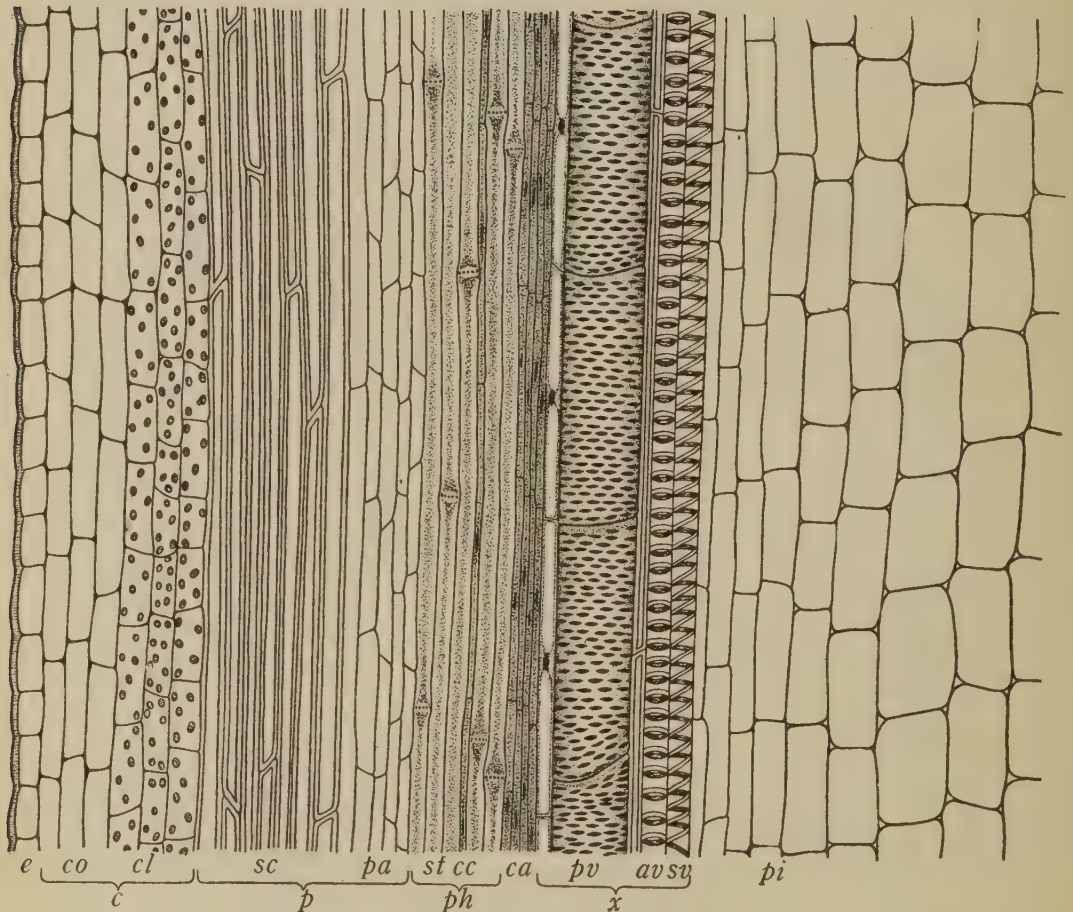


FIG. 115. Longitudinal section of a portion of a stem of *Aristolochia elegans*  
*e*, epidermis; *c*, cortex; *co*, collenchyma; *cl*, chlorenchyma; *p*, pericycle; *sc*, sclerenchyma; *pa*, parenchyma; *ph*, phloem; *st*, sieve tube; *cc*, companion cell; *ca*, cambium; *x*, xylem; *pv*, pitted vessel; *av*, annular vessel; *sv*, spiral vessel; *pi*, pith. ( $\times 190$ )

The parenchyma cells in the cortex of a stem are near enough to the light so that some or all of them develop chloroplastids and perform photosynthesis.

By being distended with water (turgid), parenchyma cells frequently help in giving rigidity to an organ. This function of parenchyma cells is important in succulent stems and in the young parts of the stems of woody plants before strong



mechanical tissues have been developed. The rigidity produced by the turgor of the parenchyma cells is particularly useful in maintaining the form of the younger parts of herbaceous and climbing stems. It is of little or no help in dicotyledonous stems that have developed a massive column of wood.

Parenchyma cells serve for the slow conduction of water and food. In the case of the cortex of the stem it is evident that the water which is received by the collenchyma and the epidermis must be conducted through the parenchyma.

The parenchyma is the special storage tissue of plants. In general the parenchyma of the cortex is less important than the parenchyma of the stele as a food-storage tissue, but food is frequently stored in it to some extent.

**Collenchyma.** On the inside of the epidermis there is usually a band of collenchyma (Figs. 113-115).

The cells of the collenchyma are modified parenchyma cells with cellulose walls thickened at the angles where three or more cells are in contact (Fig. 25). The collenchyma resembles parenchyma in being alive and in having a moderate amount of protoplasm. The chief function of collenchyma cells is to serve as strengthening material in succulent organs which do not develop much woody tissue, or in the soft young parts of woody plants before stronger tissues

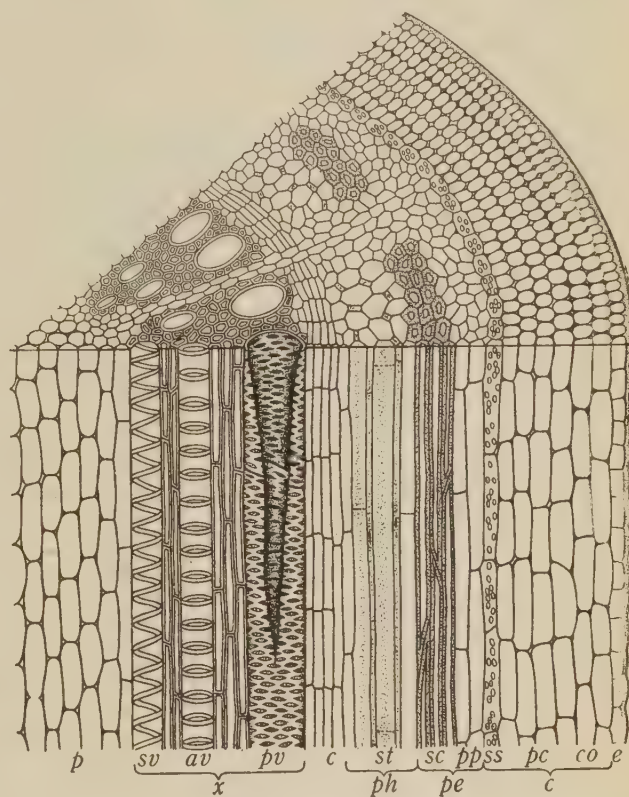


FIG. 116. Diagrammatic combined cross and longitudinal sections of stem

*p*, pith; *x*, xylem; *sv*, spiral vessel; *av*, annular vessel; *pv*, pitted vessel; *c*, cambium region; *ph*, phloem; *st*, sieve tube; *pe*, pericycle; *sc*, sclerenchyma; *pp*, parenchyma; *c*, cortex; *ss*, starch sheath; *pc*, parenchyma of cortex; *co*, collenchyma; *e*, epidermis

have been developed. They are especially fitted for giving strength to young, growing organs, since the thickened parts of the walls have considerable rigidity, while the thinner parts allow for an exchange of materials between cells and for the stretching and growth of the cells. The collenchyma cells of stems sometimes contain chloroplastids and carry on photosynthesis.

**Sclerenchyma.** Thick-walled dead cells known as sclerenchyma are found in the cortex of some stems. There are two varieties of



FIG. 117. Wood fibers from an oak (*Quercus bennettii*). ( $\times 40$ )

these sclerenchyma cells: short or irregularly shaped cells, known as stone cells, and sclerenchyma fibers. Sclerenchyma fibers are long, dead, thick-walled cells and serve as strengthening material. Stone cells give stiffness to the cortex and, when they form a more or less continuous layer, may take the place of the epidermis after the part of the cortex which is exterior to them has disappeared.

**Stele of dicotyledonous plants.** The part of the stem inside of the cortex is known as the stele (Figs. 113-115). This consists of three general regions.

In the center is the *pith*, composed of thin-walled parenchyma cells. This pith is surrounded by the *vascular-bundle region*, which is composed of *vascular bundles* separated by radial rows of parenchyma cells known as *pith rays*. Outside of this is the *pericycle*.

**Pith.** In a dicotyledonous plant the center of the stem is composed of thin-walled parenchyma cells and is known as the pith (Figs. 113, 115). The cells of the pith are very similar to other parenchyma cells and have the same general functions. As they are not exposed to the light, they do not develop chloroplastids and so do not perform photosynthesis. In perennial plants the pith is frequently a transitory structure.

**Vascular bundles.** Around the pith are compact groups of cells which, as seen in cross section, are arranged in the general form



of a broken ring (Fig. 113). Each of these groups is a vascular bundle. A vascular bundle of a dicotyledonous stem consists of three parts (Figs. 113–116). The region nearest the center of the stem contains thick-walled cells and is known as *xylem*. The peripheral portion of the bundle is composed of thin-walled cells called *phloëm*. The xylem and phloëm are separated by a *cambium layer*, which is composed of meristematic cells. By division the cambium layer increases the size of bundles by forming xylem cells on the inner side and phloëm cells on the outer side.

**Xylem.** The xylem which is formed before the activity of the cambium has begun to produce xylem and phloëm cells is called primary xylem. This primary xylem is composed of two parts. The xylem formed first is nearest the interior of the stem and is called *protoxylem*. The more peripheral part of the primary xylem is known as *metaxylem*.

Xylem is composed of three different types of cells: namely, *tracheary cells*, which include tracheids and vessels; *wood fibers*; and *wood parenchyma*.

**Tracheary elements.** The *tracheids* are elongated dead cells, with walls that are thick in some places and thin in others. They serve to conduct water, or both as water-conducting and as strengthening cells. The thin places in the walls allow water to pass readily from cell to cell, while the thickened portions protect the cells from being crushed by the pressure of the surrounding tissues. As the tracheids are dead cells and without protoplasmic contents, they cannot develop turgidity, and so, if the walls were uniformly thin, the pressure of the

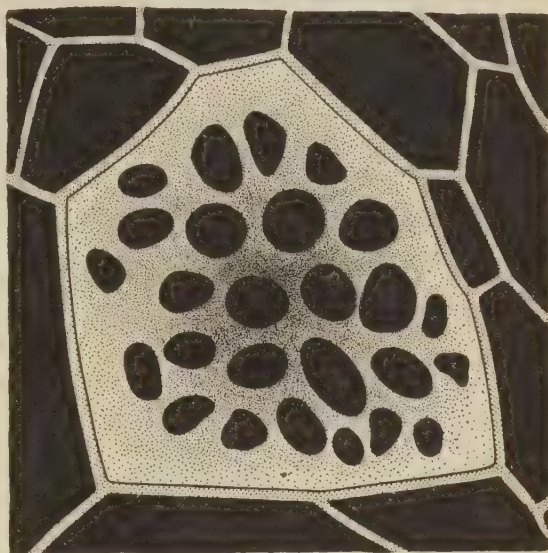


FIG. 118. A sieve plate of a squash stem (*Cucurbita maxima*) pierced by holes, walls of sieve tube, and surrounding cells. ( $\times 110$ )

neighboring cells would cause them to collapse. The walls of the tracheids are heavily impregnated with lignin. This material serves to strengthen them without greatly interfering with their permeability.

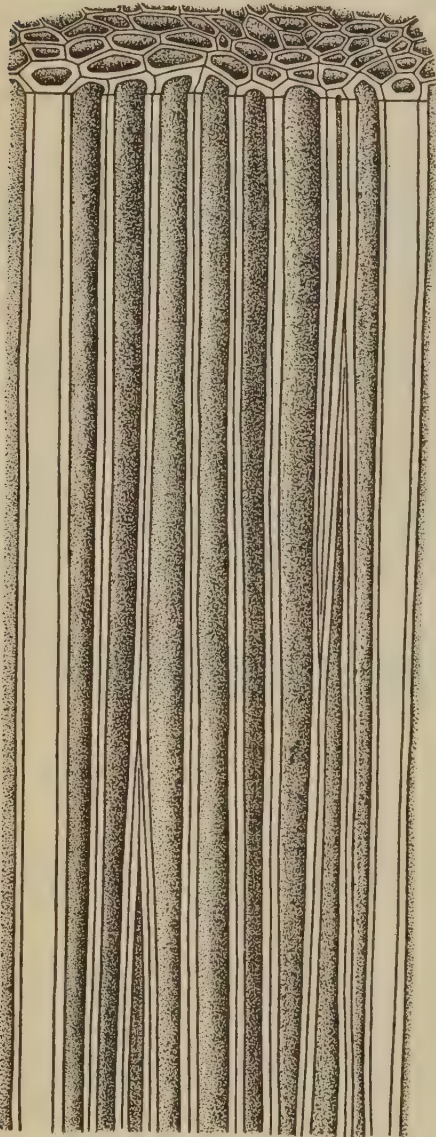


FIG. 119. Sclerenchyma fibers from a leaf of a century plant (*Agave cantula*).  
( $\times 300$ )

*Vessels* are composed of rows of tracheary cells the cavities of which are connected by the total or partial disappearance of the cross walls. The diameter of vessels is usually much greater than that of tracheids, and, as they form long tubes, they constitute the principal water-conducting elements of the dicotyledonous stem.

Tracheary cells may be divided into several types according to the method by which the walls are thickened (Figs. 115, 116). *Annular* tracheary cells have thickenings in the form of rings, while *spiral* tracheary cells have spiral thickenings. *Pitted* tracheary cells have walls which are uniformly thickened except for thin places in the form of pits. When the pits are long and narrow and lie horizontally one above the other, the tracheid or vessel is said to be scalariform, owing to the ladderlike appearance of the thickenings.

The protoxylem is composed largely of annular and spiral vessels and parenchyma, while the tracheary elements of the secondary xylem are pitted. Protoxylem is differentiated while the stem is elongating, and so the spiral and annular thickenings of the vessels are of special advantage, as they allow the vessels to be stretched. The metaxylem and secondary xylem are formed after increase in length has ceased, and therefore



pitted tracheary cells are advantageous, as they have greater strength than spiral and annular ones.

**Wood fibers.** These are long, slender, pointed, dead cells with greatly thickened walls and only comparatively few small pits (Fig. 117). They serve as strengthening cells. Tracheids that have a structure approaching that of wood fibers are called fiber tracheids. These two types of fibers usually make up a considerable proportion of the wood of dicotyledonous trees.

**Wood parenchyma.** Parenchyma cells in the xylem are designated as wood parenchyma. They serve chiefly for the storage of food.

**Phloëm.** The primary phloëm of the dicotyledonous stems consists of three types of cells: sieve tubes, companion cells, and phloëm parenchyma.

**Sieve tubes.** The sieve tubes consist of thin-walled, elongated cells arranged in vertical rows (Figs. 115, 116). The adjacent cells of a sieve tube are united by small holes in the cross walls (Fig. 118). Also, sieve tubes have rounded places on the side walls which are pierced by small holes and connect one sieve tube with another or with a companion cell. The areas on the walls of sieve tubes which contain such holes are called sieve plates. The sieve tubes get their name from the sievelike appearance of these plates. The walls of the sieve

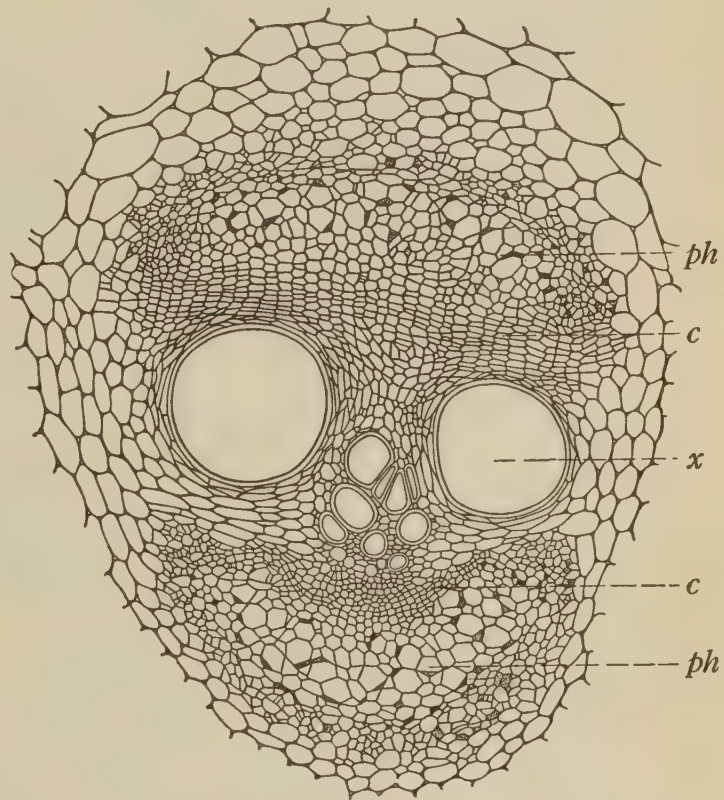


FIG. 120. Cross section of a bicollateral bundle of a squash stem, showing phloëm on both sides of the xylem

*ph*, phloëm; *c*, cambium region; *x*, xylem vessel.  
(× 95)

tubes are lined with a layer of protoplasm, but mature sieve tubes do not contain any nuclei.

The sieve tubes serve primarily for the conduction of food material. The holes which connect the cells of the sieve tubes make these tubes especially suited to the conduction of protein.

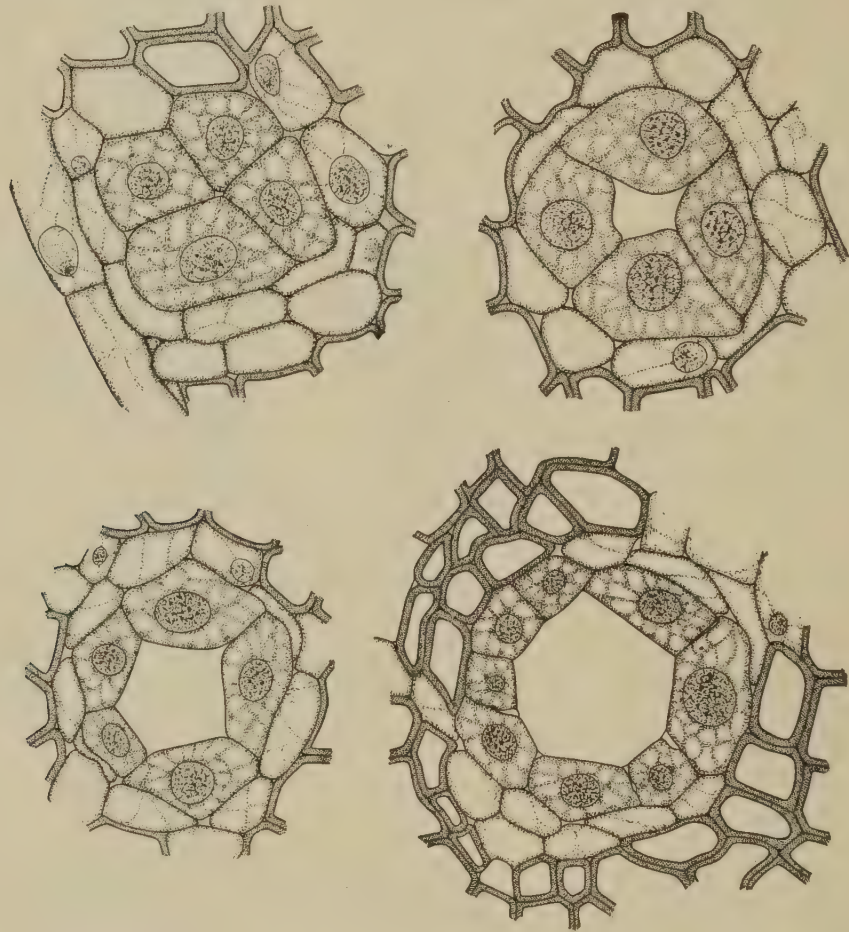


FIG. 121. Successive stages in the formation of a resin duct in pine. ( $\times 250$ )

**Companion cells.** The companion cells are small cells which are attached to the sieve tubes. Each companion cell is the sister cell of a sieve-tube cell, the two being formed by the division of a mother cell. The exact function of the companion cells is more or less obscure, but since they are connected by sieve plates with the sieve tubes which contain protoplasm but no nuclei, it would appear that the nuclei of the companion cells serve as nuclei for the sieve tubes. The small shaded cells in the phloem in Fig. 114 are companion cells.



**Phloëm parenchyma.** The phloëm contains parenchyma cells whose structure is very similar to that of other parenchyma cells. These are known as phloëm parenchyma.

**Cambium.** While the other cells of the stem which are formed at the tip are being differentiated into permanent tissue, a single layer between the xylem and phloëm remains undifferentiated (Figs. 113-116). This layer of meristematic cells is known as the cambium. The cambium consists of a single layer of cells which, by division, gives rise to xylem cells toward the center of the stem and phloëm cells toward the periphery. The activity of the cambium cells thus enlarges the size of the bundles and, in consequence, that of the stem. This process is known as secondary thickening and will be discussed in detail in a later section.

At first the cambium is confined to the bundles, but later the parenchyma cells of the pith rays which lie between the edges of the cambium in the bundles divide and form a layer of cambium which reaches across the pith rays and connects that in the bundles, so that the cambium becomes a continuous cylinder (Fig. 139). The beginning of this process is shown in Fig. 113.

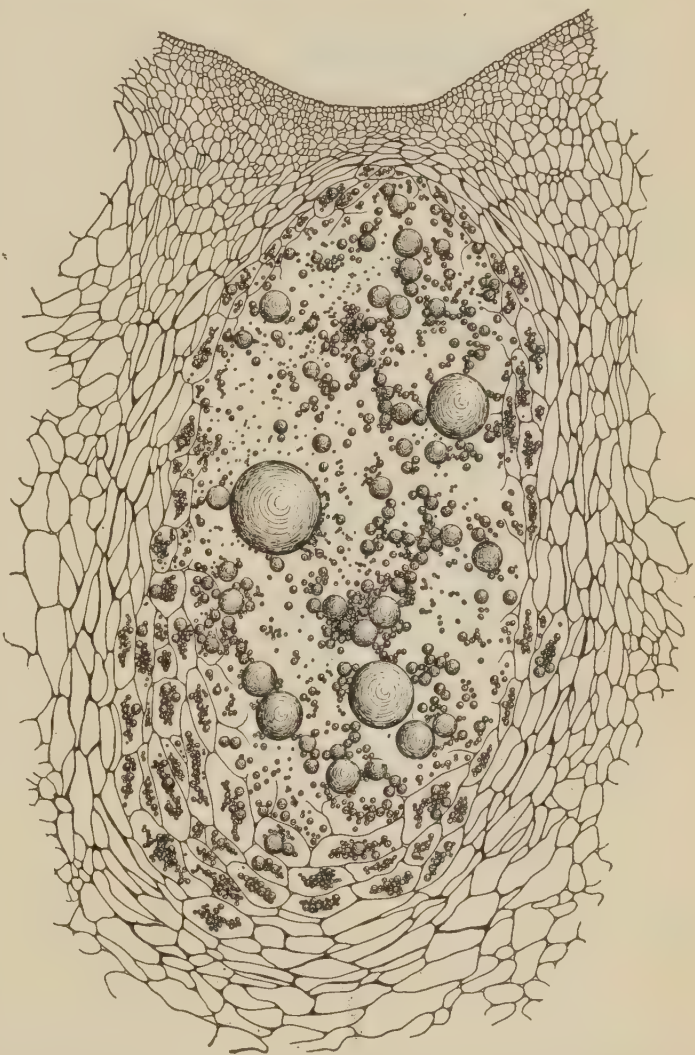


FIG. 122. Longitudinal section of oil gland in orange peel. ( $\times 450$ )

**Pith rays.** The vascular bundles are separated from each other by radial rows of parenchyma cells (Figs. 113, 116) known as pith rays.<sup>1</sup> The pith-ray cells are usually elongated in a radial direction. They serve primarily for the conduction of food and water radially in the stem and for the storage of food. Food



FIG. 123. Latex tube of poinsettia (*Euphorbia pulcherrima*). ( $\times 125$ )

material which is stored in the wood parenchyma is conducted to these cells by the pith rays. The pith rays also serve for the conduction of water from the xylem toward the other parts of the stem. If a pith ray from an old stem is stained with iodine, it will usually be found to contain numerous starch grains.

**Pericycle.** The region between the vascular bundles and the cortex is known as the pericycle. It is usually composed of parenchyma and sclerenchyma cells, but the sclerenchyma cells

may be absent. The sclerenchyma may occur as separate patches (Figs. 114, 116) or as a continuous ring in the outer part of the pericycle (Fig. 113), forming a sharp line of demarcation between the stele and the cortex. The sclerenchyma cells in the pericycle

<sup>1</sup> The term *wood ray* is proposed in place of *pith ray* by some modern anatomists, on the ground that these rays do not belong to the pith, but that the parts of the rays between the primary xylem represent tracheids which have been transformed into parenchyma cells. Owing to the widespread use of the term *pith ray* in literature it seems convenient to retain it, even though, from the standpoint of origin, it may be inappropriate.



are like other sclerenchyma cells (Fig. 119) in being long, thick-walled dead cells which serve as strengthening material.

**Variations in stem structure.** The above description of the structure of stems applies to the great majority of dicotyledonous plants, but there are a few which show minor variations. If these few exceptional cases are left out of consideration, the general structure of dicotyledonous stems is remarkably uniform. The relative development of the various parts, however, varies greatly in different species. In some cases the pith is wide, while in others it is narrow. It may be wide and transitory and its early disappearance result in a hollow stem. The vascular bundles vary considerably in number and size, while the pith rays and cortex vary in width. Thus, while there is a remark-

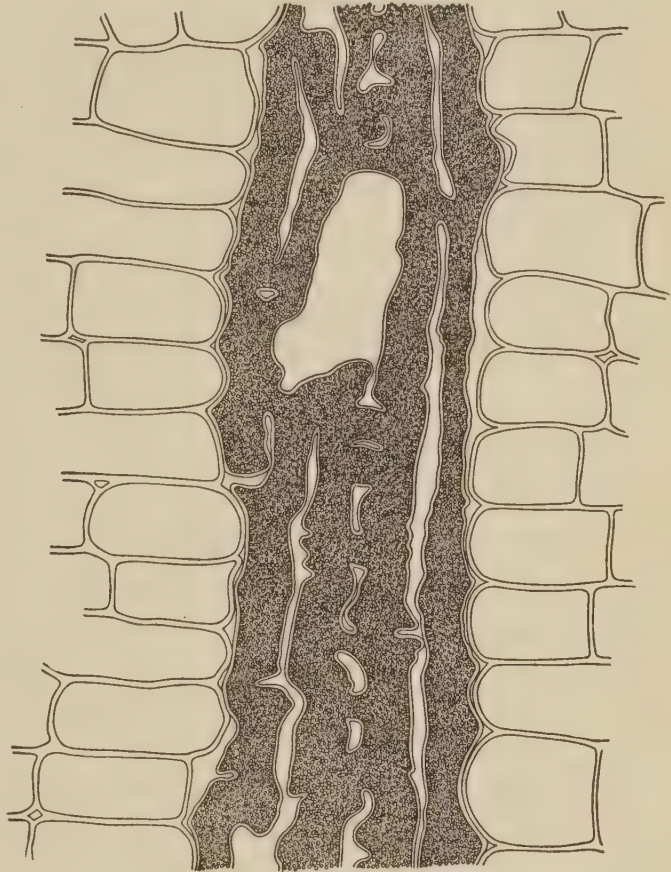


FIG. 124. Network of latex tubes of a rubber tree (*Manihot glaziovii*)

able uniformity in the general plan of the dicotyledonous stem, there are at the same time considerable differences in detail.

Bundles which have the phloëm only on the outside of the xylem are called *collateral* bundles. The bundles of some plants have phloëm on both the outside and the inside of the xylem (Fig. 120) and are known as *bicollateral* bundles.

**Resin ducts.** Many plants contain intercellular passages filled with resinous substances and known as resin ducts. They are formed either by the separation of neighboring cells (Fig. 121) or by the disintegration of cells. Turpentine is obtained by cutting

through the resin ducts of pine trees, after which the turpentine exudes and is collected. Various kinds of varnish and other resins are obtained by the same method from other trees.

Resin ducts are, essentially, long passages surrounded by glandular cells. They occur not only in stems but also in other parts of plants.

**Internal glands.** Resin canals are one type of internal gland, of which a number of other forms occur in various plant organs. Internal glands frequently contain essential oils. These oils are volatile and are usually very odoriferous. Well-known examples are eucalyptus oil and the oil from orange peel. The latter occurs in large oval glands. These glands originate in the splitting apart of certain cells, but are formed largely by the breaking down of cells containing the oil. The disintegration of the cells brings the oil into the large cavity of the gland (Fig. 122).

**Latex tubes.** Milky juice (latex) is found in long, branching tubes known as latex tubes (Fig. 123). In many cases neighboring tubes become connected, thus forming a network (Fig. 124). When these tubes are cut, the latex exudes as a white, watery juice with a milky appearance. Rubber, gutta-percha, opium, gum chicle (the chief base of chewing gum), and other valuable substances are derived from coagulated latex. The tapping of rubber trees consists in cutting the tubes and allowing the latex to exude.

Latex tubes are formed in two very different ways. In some cases rows of cells lose their cross walls and become transformed into latex tubes, as in Pará rubber (*Hevea brasiliensis*). In other cases the tubes are not part of the tissues produced from either the apex of the stem or the cambium, but result from the growth of tubes found in the seedling. As the stem grows in length, or as other organs are formed, these latex tubes also grow and push their way between the cells of the newly formed tissues.



## SUMMARY OF PRINCIPAL TISSUES IN A DICOTYLEDONOUS STEM

- Epidermis
  - Epidermal cells
  - Guard cells
  - Trichomes
- Cortex
  - Collenchyma
  - Parenchyma
  - Starch sheath
- Stele
  - Pericycle
    - Parenchyma
    - Sclerenchyma
  - Pith rays
    - Parenchyma
  - Pith
    - Parenchyma
  - Vascular bundles
    - Phloëm
      - Sieve tubes
      - Companion cells
      - Phloëm parenchyma
    - Cambium
      - Meristematic cells
    - Xylem
      - Tracheary cells
        - Vessels and Tracheids { Spiral
        - { Annular
        - { Pitted
      - Wood fibers
      - Wood parenchyma

## ANATOMY OF MONOCOTYLEDONOUS STEMS

Monocotyledonous stems are similar to dicotyledonous stems in having an epidermis, a cortex, and a stele. The cortex may be well developed and sharply marked off from the stele, or it may be very narrow and inconspicuous (Fig. 125). It is in

the structure and arrangement of the bundles that monocotyledonous stems differ markedly from dicotyledonous stems.

**Stele.** The vascular bundles of monocotyledonous stems, instead of being arranged in a cylinder as in dicotyledonous

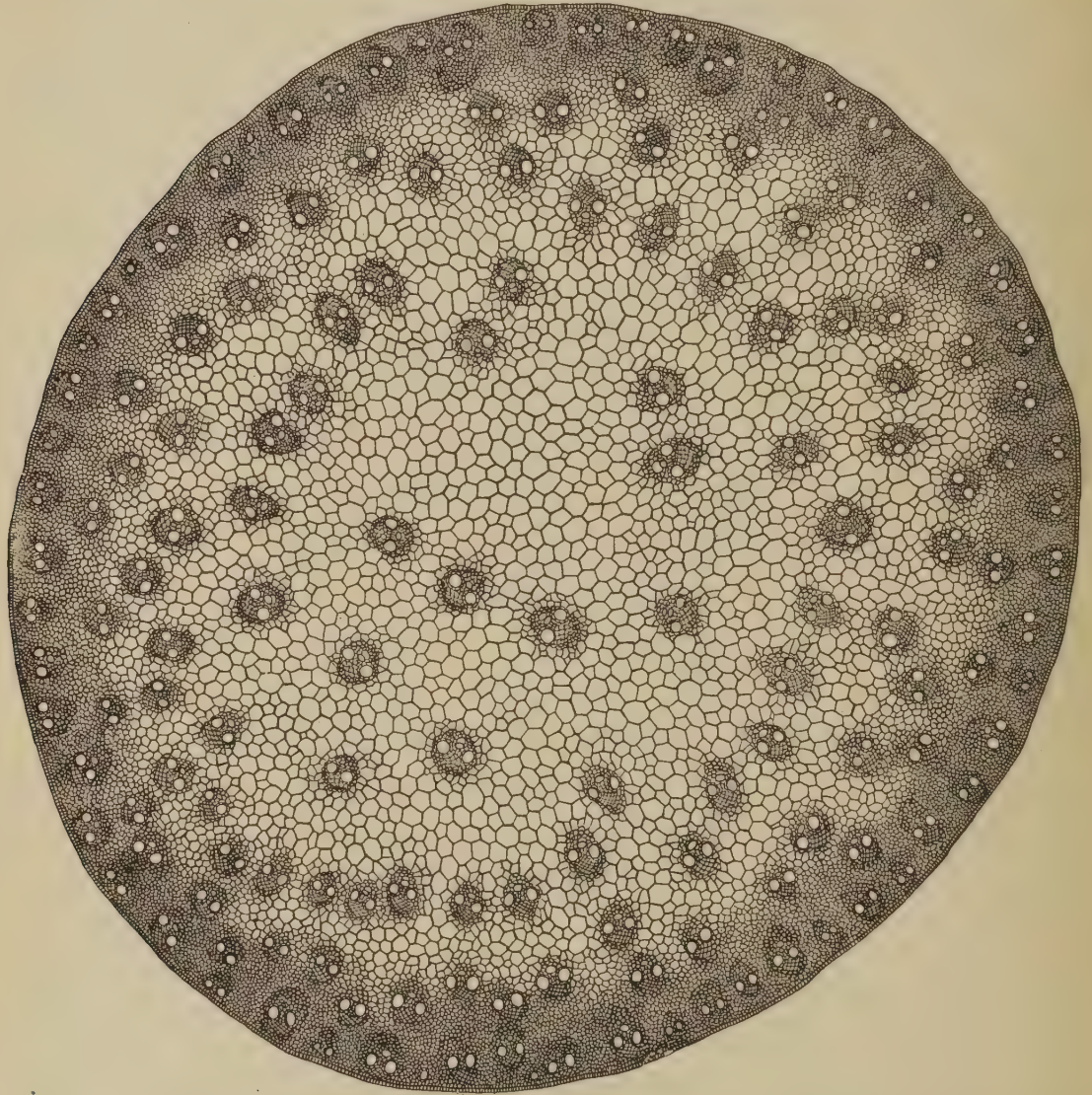


FIG. 125. Cross section of a monocotyledonous stem, *Saccharum spontaneum*  
The dark oval areas are cross sections of vascular bundles. ( $\times 25$ )

stems, are usually scattered throughout the stele, including the pith, so that there is no distinction between pith and pith rays (Figs. 125, 126). Sometimes the center of the stele is free from vascular bundles and is occupied by parenchyma cells, which dry up and disappear at an early stage, resulting in a hollow stem, as in most grasses, including most bamboos.



**Vascular bundles.** The vascular bundles of monocotyledonous stems are like those of dicotyledonous stems in consisting of xylem toward the center of the stele and phloëm toward the periphery. They differ, however, in not having a cambium layer, such as is found in dicotyledons (Fig. 127). This is

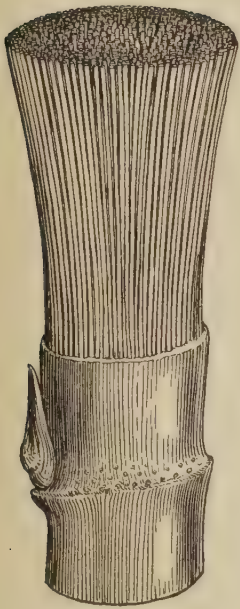


FIG. 126. Vascular bundles dissected out of an internode of sugar cane. ( $\times \frac{1}{2}$ )

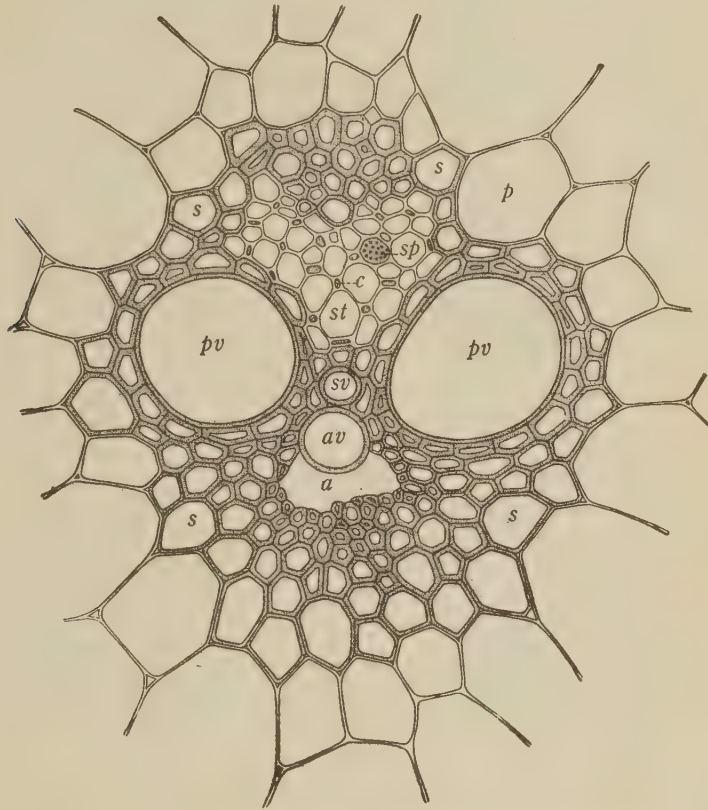


FIG. 127. Cross section of a vascular bundle of sugar cane (*Saccharum officinarum*)

*p*, parenchyma; *s*, sclerenchyma of bundle sheath; *a*, air space; *av*, annular vessel; *sv*, spiral vessel; *pv*, pitted vessel; *st*, sieve tube; *sp*, sieve plate; *c*, companion cell. ( $\times 185$ )

connected with the fact that monocotyledons usually do not have secondary thickening. Each bundle is generally more or less completely surrounded by a sheath of sclerenchyma cells, the *bundle sheath* (Figs. 127, 128), which is particularly well developed on the sides toward the center and toward the periphery of the stem. The phloëm consists mostly of sieve tubes and companion cells, and the xylem of vessels and wood parenchyma.

The strands of sclerenchyma around the bundles of some plants are extracted and used in various ways as fibers. Maguey and sisal fibers are the strands of sclerenchyma around the bundles of the leaves of species of *Agave* (Fig. 119), while

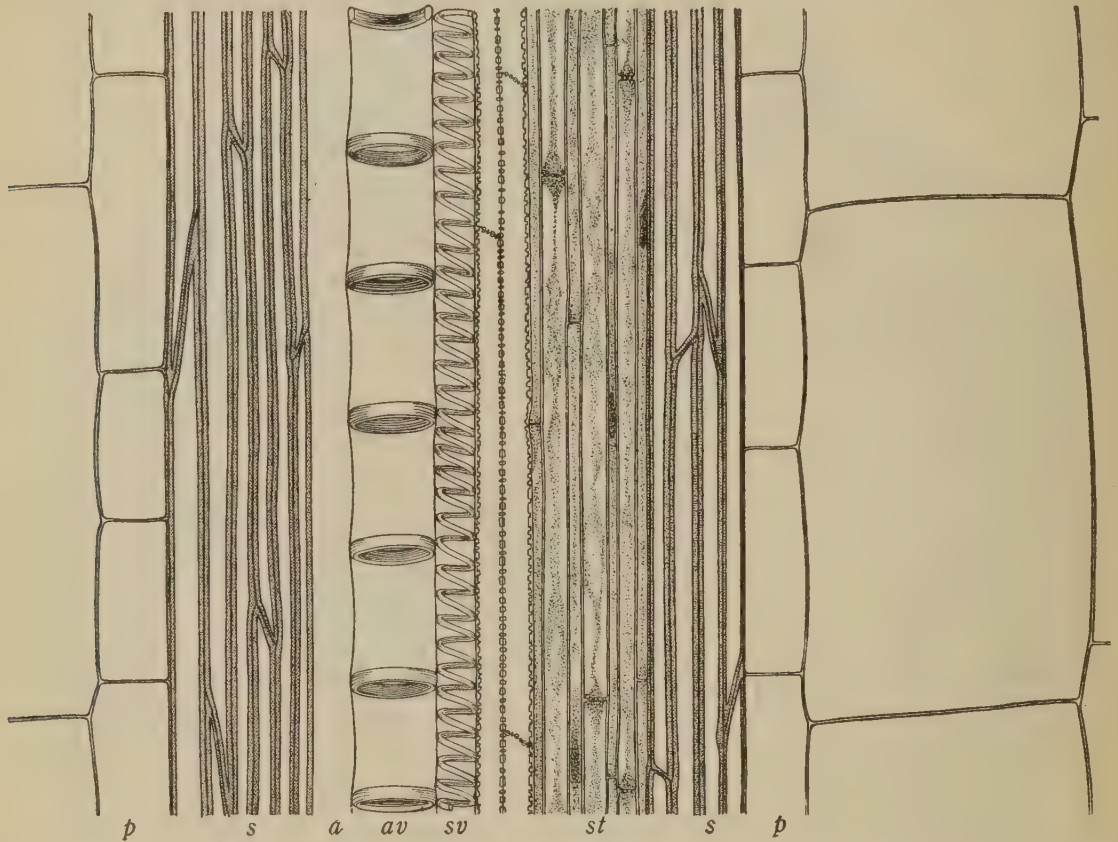


FIG. 128. Longitudinal section through a vascular bundle of sugar cane (*Saccharum officinarum*)

*p*, parenchyma; *s*, sclerenchyma of bundle sheath; *a*, air space; *av*, annular vessel; *sv*, spiral vessel; *st*, sieve tube. ( $\times 150$ )

abacá (Manila hemp) is composed of similar strands from the leaf bases of *Musa textilis*, a plant which is almost identical with the banana in appearance.

The arrangement of the different elements in the bundles of corn and sugar cane is characteristic of many monocotyledonous bundles (Figs. 127, 128). In these cases the bundles are surrounded by a sclerenchyma sheath which is widest on the sides toward the center and toward the periphery of the stem. On the side near the interior of the stem, just within the bundle sheath, there is usually a conspicuous air space. Next to this



there are frequently two elements of the protoxylem; the first is an annular vessel and the second is a spiral vessel. On both the right and the left side of the bundle is found a large vessel which is pitted or narrowly reticulate. Between the larger vessels are smaller, tracheary elements. The phloëm is next to the peripheral part of the bundle sheath and contains conspicuous sieve tubes and companion cells.

The number of vessels varies in monocotyledonous bundles. In many cases there is only one large vessel, instead of two as in corn and sugar cane.

#### COURSE OF BUNDLES IN STEMS

A bundle extends up the stem and then passes out into a leaf. The bundles from leaves in the upper part of the stem enter the stem, pass down, and at a lower node join with other bundles. In this way the vascular elements in the stem become connected with new leaves. At the nodes bundles branch, while branches of different bundles coalesce (Fig. 129).

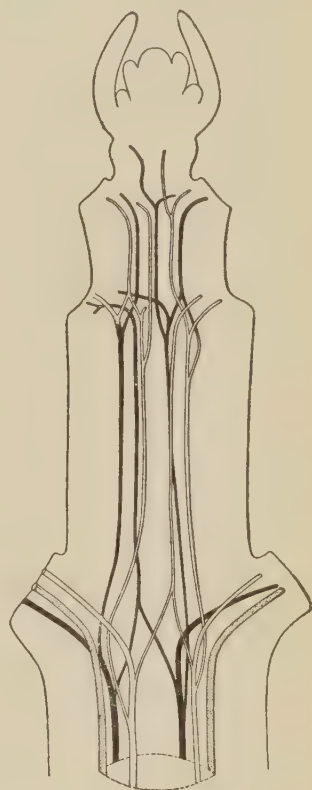


FIG. 129. Course of bundles in stem of *Clematis verticellaris*

Modified after Nagali

#### ANATOMY OF CONIFEROUS STEMS

In coniferous stems the general arrangement of the various tissues is very similar to that in dicotyledonous stems. The same type of secondary thickening occurs in both kinds of stems. The most conspicuous differences are that the xylem of conifers contains only tracheids and wood parenchyma, and that companion cells are not found in the phloëm.

Since the xylem of conifers does not contain fibers or vessels (Fig. 130), the tracheids serve both as water-conducting and as strengthening elements. Tracheids are not so well fitted for conducting water as are vessels. The small size and xerophytic

structure of coniferous leaves (Fig. 475) probably have some connection with the absence of vessels in coniferous stems.

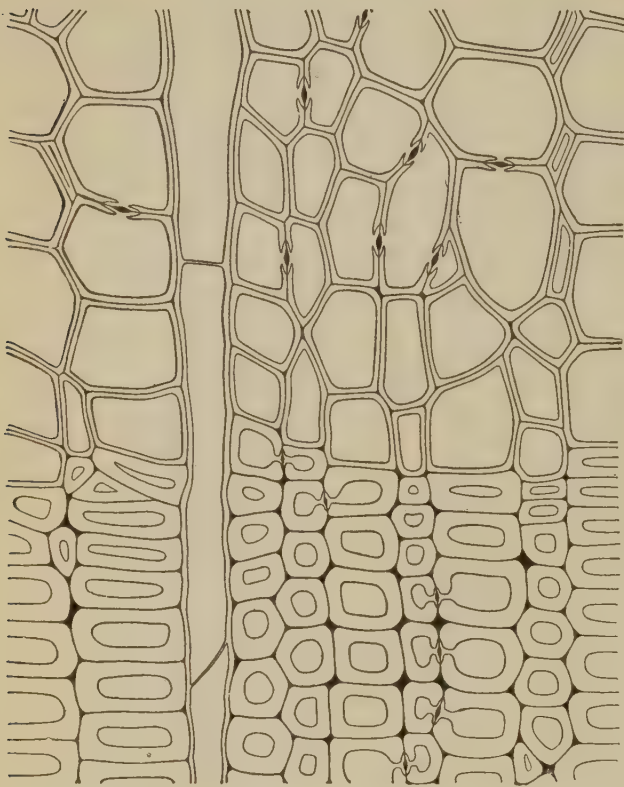


FIG. 130. Cross section of a small portion of the wood of a redwood tree, showing xylem on both sides of a pith ray

The small cells in the lower part of the drawing are the last of the wood cells formed during a summer, while the large cells above them are the first xylem cells formed during the next spring. The fact that much larger cells are formed in the spring than later in the summer results in the marking of the wood by annual rings of growth. ( $\times 275$ )

ably connected with the ability of these trees to retain their foliage throughout the cold winter. At such times coniferous trees have some advantage over dicotyledonous ones in that they can carry on photosynthesis. In the tropics conifers very rarely occur at low elevations, while they flourish in high mountainous regions where the rate of evaporation is always low.

Most coniferous trees (Figs. 477, 478, 498) retain their leaves for several years, — in temperate countries throughout the long, cold winter, when the dicotyledonous trees lose their leaves. In the discussion of leaves it was pointed out that the loss of leaves by deciduous trees is a method of restricting the rate of transpiration at times when the roots are not able to absorb enough water to replace that which would be lost by the foliage. The deciduous tree without its leaves is one of the most perfectly protected of plant structures, since all the exposed portions are effectively covered by the impervious bud scales and bark. The low rate of transpiration from coniferous leaves is proba-



## ARRANGEMENT OF MECHANICAL TISSUES

**Mechanical tissues.** The plant body obtains strength from three general types of cells:

1. *Parenchyma cells*, whose rigidity is due almost entirely to osmotic pressure. Parenchyma tissue is weak and so must be present in considerable bulk in order to give any great amount of strength.

2. *Collenchyma cells*, which are living cells and have their walls thickened at the angles where three or four cells meet (Fig. 25). These cells get their rigidity from the thickened walls, as well as from turgor, and are therefore much better strengthening material than are parenchyma cells. As they are living cells whose walls can be stretched, they are especially fitted for strengthening the growing portions of a plant.

3. *Thick-walled dead cells* (Figs. 117, 119), including the sclerenchyma of the cortex and pericycle and the wood fibers. The wood fibers are elongated dead cells with very thick walls. Sclerenchyma cells are stronger than parenchyma or collenchyma cells and are the principal strengthening material of old stems. As they are dead cells with very thick walls, they are not suited to give strength to growing parts. Thick-walled tracheids may be very similar to sclerenchyma in their mechanical property.

**Girders.** The arrangement of the strengthening material is different in leaves, in stems, and in roots, and is suited to the special stresses which these various organs have to withstand. In order to understand this arrangement it will be convenient to consider the stresses occurring in a girder, or beam. If a beam of wood or other material is supported at both ends and weighted in the middle, the upper surface will be subjected to compression and the lower surface to tension, or stretching. Going from the upper surface to the lower, we find that the compression decreases as the center is approached and at the center it becomes zero. The stress is then changed to tension, which gradually increases toward the lower surface. It will thus be seen that the greatest stresses in a beam are at the upper and lower surfaces and the

least stress is in the center. For this reason it is usual to construct a beam in such a manner that it is more massive or composed of stronger material at the upper and lower surfaces than in the center. A usual form is the *I-beam* (Fig. 131). In this case the material is expanded at the upper and lower surfaces and connected by a much narrower portion. The extensions at the surfaces are called *flanges*. In bridge construction the connecting portion, known as the *web*, is frequently made of latticework.

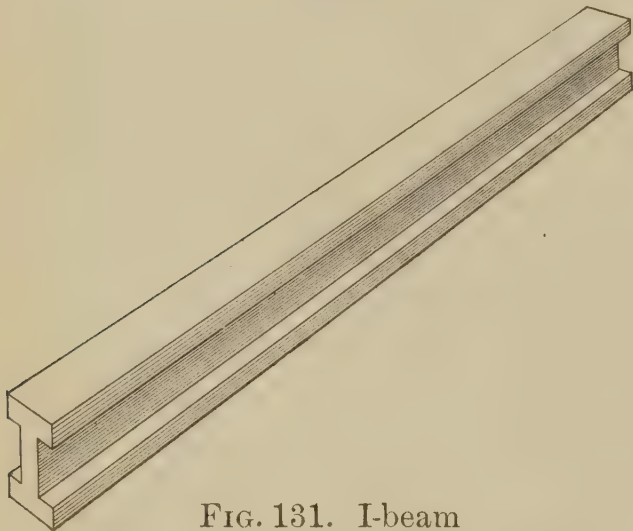


FIG. 131. I-beam

The wide portions at the top and bottom are the flanges; the narrow connection is the web

stresses are at the upper and lower surfaces and the least stress is in the center. This arrangement, therefore, calls for longitudinal girders in which the strongest material is near the outer surfaces. The midrib and larger veins of the leaf represent the girders. The principal strengthening material in these is usually collenchyma, and this is generally found as a broad band near the upper and lower surfaces just within the epidermis (Fig. 24). The collenchyma, therefore, represents the flanges of an I-beam, while the tissues between the two bands of collenchyma represent the web. The larger veins of grasses usually have sclerenchyma near the upper and lower surfaces, and so act as girders (Fig. 31).

**Mechanical tissues in stems.** If a column, such as a tree trunk, were supporting an evenly distributed weight, the manner in

**Mechanical tissues in leaves.** In a leaf we have different conditions from those just discussed, in that the leaf is supported at only one end. The weight of the leaf gives it a tendency to bend downward so that its upper surface is stretched, or under tension, while its lower surface is under compression. As in the other case, the greatest



which the strengthening material was arranged would, theoretically, make comparatively little difference. The only stress

would be a downward pressure, or compression, the resistance to which would depend more on the cross-sectional area than on the arrangement of the strengthening material. Actually, however, such a condition is seldom attained; for the column, be it the stem of a plant or the support of a building, rarely remains permanently vertical. When the stem of a plant becomes inclined, as by the action of the wind or by the weight of the branches, the side that is uppermost tends to become stretched, or

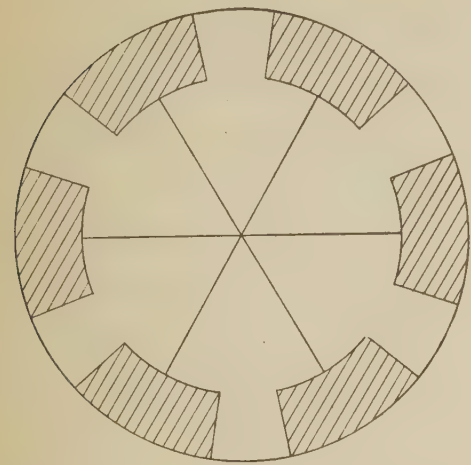


FIG. 132. Diagram of cross section of a compound girder composed of I-beams, the webs of which have a common center

develops tension, while the lower side is subjected to compression. It therefore becomes important to have the strengthening material distributed near the upper and lower surfaces, or, in other words, in the form of an I-beam. As the plant is likely to bend in any direction, however, and thus may develop stress on any side, it is advantageous to have a number of these girders, with the webs crossing each other and the center of each at the center of the stem (Fig. 132). In the four-cornered stems of such plants as the mints or coleus the corners are occupied by a conspicuous development of collenchyma (Fig. 133), which thus forms the flanges of two I-beams, the webs of which are crossed. In many plants there are strands of sclerenchyma outside of each vascular bundle (Fig. 134), and in such cases two



FIG. 133. Diagram showing arrangement of vascular bundles and collenchyma (dotted area) in a four-cornered stem

strands on opposite sides of the stem represent the flanges of an I-beam. This sclerenchyma, which is near a bundle, not only serves as one of the flanges of an I-beam but also is in a position to protect the delicate elements of the phloëm. When the edges of the flanges of such a compound girder as that shown in Fig. 132 are connected, there is no necessity for the webs; and if they are absent, a hollow cylinder results. This type of construction is very frequently found in plants and is particularly

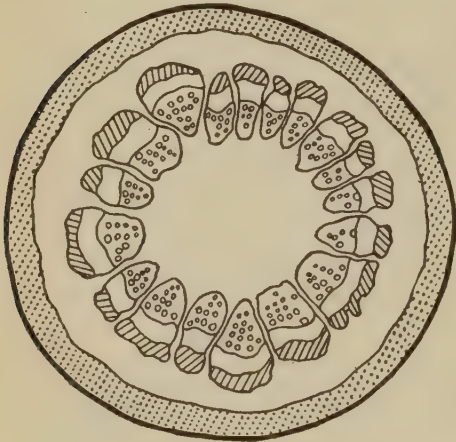


FIG. 134. Diagram of a dicotyledonous stem, showing sclerenchyma (hatched areas) just outside of each bundle, and collenchyma (dotted area) forming a hollow cylinder within the epidermis

evident in hollow stems, such as those of most grasses. In many plants the sclerenchyma is arranged in the form of a hollow cylinder (Figs. 113, 135). Such hollow cylinders are, as a rule, near the outer surface of the stem. The strengthening material of the growing part of a stem is usually collenchyma, and this is generally arranged in the form of a hollow cylinder just within the epidermis (Figs. 134, 135).

The foregoing discussion of the arrangement of the strengthening material in the stem applies particularly to herbaceous and young stems. In the case of trees the de-

velopment of a massive column of wood takes the place of the strengthening material that was used in the young stem.

**Tissue tensions.** The location of thick-walled mechanical cells near the periphery of an organ with thin-walled parenchyma cells in the center gives rigidity in another manner besides that just considered. Thick-walled cells, particularly dead sclerenchyma cells, offer considerable resistance to any tendency to stretch them. On the other hand, thin-walled parenchyma cells tend to stretch, owing to their turgidity. The stretching of the parenchyma is, however, checked by the strong, thick-walled cells, which are themselves under tension, owing to the tendency of



the parenchyma to stretch them. These two strains, working against each other, produce rigidity in somewhat the same way

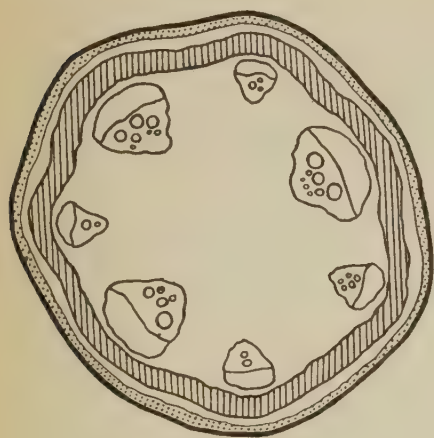


FIG. 135. Diagram of a dicotyledonous stem with a sclerenchyma ring (hatched area) outside of the vascular bundles and a ring of collenchyma (dotted area) just within the epidermis

as in a turgid cell, in which the contents, which have a tendency to swell, are compressed by the stretched cell wall, or as in a rubber tube when air or water is compressed within the tube. The compression of inner by outer tissues can very easily be demonstrated with stems or petioles of many herbaceous plants. Fig. 136 shows a piece of a large petiole which was cut off evenly at both ends, after which the outer and inner parts were separated at the upper end by a cylindrical cut. The central portion, which was under compression, being freed from the

outer part, elongated and so projected beyond the latter, which contracted slightly.

**Mechanical tissues in monocotyledonous stems.** In many monocotyledonous plants the arrangement of the strengthening material is very similar in principle to the reënforcing of concrete in a concrete structure. The concrete withstands compression, while the iron rods withstand the tension due to movement etc. In monocotyledonous plants the parenchyma withstands the compression, while the sclerenchyma strands, which are connected with the vascular bundles, withstand the tension (Fig. 125).

A very excellent example of this is abacá, or Manila hemp. This plant, whose appearance and structure are almost identical with those of the banana (Fig. 66), has a massive trunklike portion



FIG. 136. Demonstration of tissue tension in a petiole of elephant's-ear (*Alocasia indica*). ( $\times \frac{2}{3}$ )

composed largely of the soft tissues of the leaf bases, through which run the long sclerenchyma strands that are the abacá of commerce. The sclerenchyma can withstand considerable tension, while the massive development of parenchyma withstands the compression.

**Mechanical tissues in roots.** The roots of a plant serve to anchor it in the ground. They act like cables, and the principal stress to which they are subjected is longitudinal tension, or pull. It is evident that when a plant is blown by the wind the roots on the side from which the wind is coming are subjected to longitudinal tension, and if they are not strong enough to withstand this they break and the plant is blown over. The best arrangement of material to withstand this type of stress is in the form of a cord. In roots the vascular bundles and strengthening materials are usually much more centrally located than they are in the stem, the center being frequently occupied by thick-walled elements. Compare Figs. 113 and 187.

#### MOVEMENT OF MATERIALS IN STEMS

**Food materials.** Proteins dissolved in water travel in the sieve tubes. The direction of the movement may be either up or down, according to where the protein is to be used or stored.

The carbohydrates travel in the phloëm. What has been said of the direction of movement of proteins applies also to the carbohydrates. The carbohydrates move from cell to cell only when they are in solution in water.

**Carbohydrates in vessels.** While carbohydrates usually move in the phloëm, they are frequently found in considerable quantities in the vessels when food material is being transported on a large scale from storage regions to rapidly growing organs, as in deciduous trees at the beginning of the period of growth, when the leaves are expanding. In such cases the carbohydrates diffuse from the parenchyma into the vessels and are carried upward to the expanding foliage or inflorescences. This is conspicuously true of the sugar maple, and explains why a solution





FIG. 137. Coconut palm with inflorescences cut and bound to be inserted in bamboo joint for collecting sweet sap



FIG. 138. Coconut palm with bamboo tubes, for collecting sweet sap, attached to inflorescence stalks



of sugar is obtained from this tree by boring into the wood in the spring. A similar phenomenon is observed in the exudation of sweet sap from tapped inflorescence stalks of palms, such as the coconut (Figs. 137, 138). Such sap is frequently used for manufacturing alcohol or sugar.

**Water.** The movement of water upward in the stem takes place in the vessels. This can be very clearly shown by cutting off a stem and placing the lower end in a colored solution. If the stem is cut across, it will be found, after sufficient time has elapsed, that the colored solution is inside the vessels. Water enters the outer cells of the roots, passes through the cortex into the stele, and enters the vessels. It then passes through the vessels of the root to those of the stem, and through these to the leaves, flowers, and fruits. The loss of water by transpiration from the chlorenchyma cells tends to increase the concentration of the contents of these cells. By osmosis and hydration of colloids the chlorenchyma cells draw water from the vessels, and so replace that which is lost through transpiration.

### SECONDARY THICKENING

**Formation of cambium.** The vascular bundles of dicotyledons contain a single layer of cambium cells, which separates the xylem from the phloëm (Fig. 113). While the other cells formed by the division of the meristem in the tip of the stem are being differentiated into permanent tissue this layer of cambium in the bundles remains meristematic. When the primary xylem and the primary phloëm are first differentiated, there is no cambium across the pith rays to connect the edges of the cambium in the bundles. After the differentiation of the primary tissues the parenchyma cells of the pith rays, which lie between the edges of cambium in the bundles, divide in a plane at right angles to the radial direction of the rays and form a layer of cambium across the pith rays. The beginning of this process is shown in Fig. 113. The newly formed cambium connects the cambium in the bundles, and this results in the formation of



a continuous ring of cambium in the region between the xylem and the phloëm (Fig. 139). In trees the region outside the cambium is known as *bark*, while that inside is known as *wood*. Usually the bark can be readily separated from the wood, as the cambium cells are soft and weak and can be easily broken.

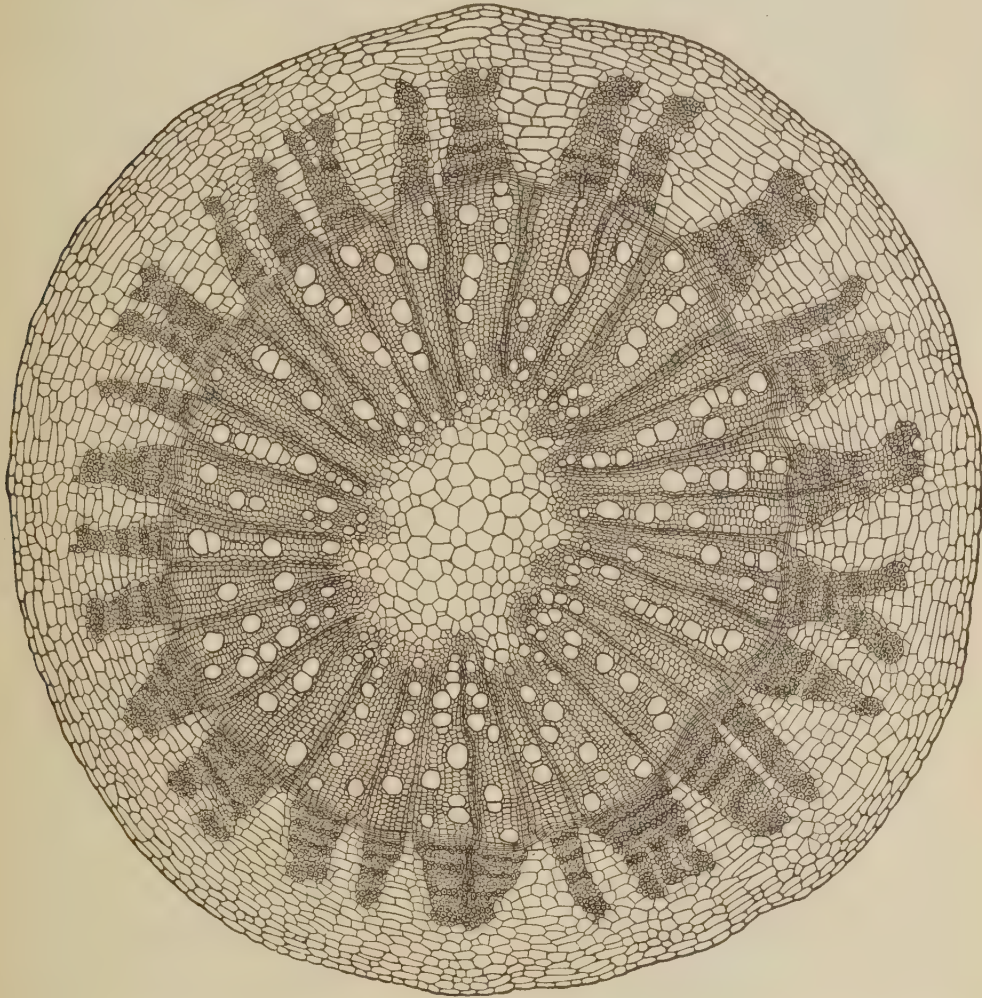


FIG. 139. A cross section of a young stem of a tropical tree, ylang-ylang (*Canarium odoratum*), in which there has been some secondary thickening. The wood is composed chiefly of wood fibers and large vessels. The bark has an alternation of bands of phloëm and strands of thick-walled bast fibers. ( $\times 40$ )

**Activity of cambium.** The cambium layer consists essentially of a single layer of cells. These cells divide in a direction parallel with the epidermis. Each time a cell of the cambium divides into two, one of the daughter cells remains meristematic, while the other is differentiated into permanent tissue. If

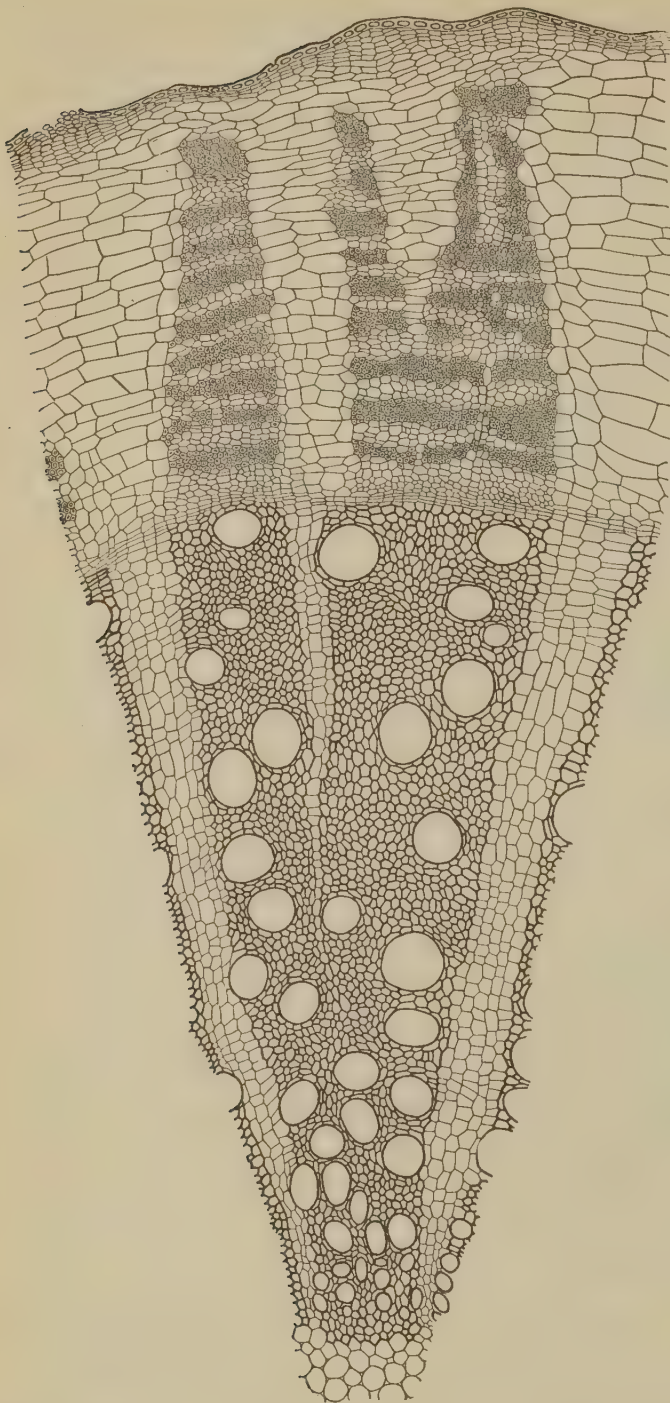


FIG. 140. A vascular bundle in a cross section of a portion of a young stem of a tropical tree (*Muntingia calabura*) which has undergone some secondary thickening

The xylem is composed largely of vessels and wood fibers. In the phloem region there is an alternation of bands of thick-walled bast fibers and thin-walled phloem cells. A secondary pith ray is shown in the center of the bundle. ( $\times 70$ )

the cell that is differentiated is next to the xylem, it forms xylem, while if it is next to the phloem, it becomes phloem. In this way new cells are added to the xylem and the phloem, and the bundles increase in size (Figs. 139, 140). While there is more or less alternation in the production of xylem and phloem cells from a cambium cell, more cells are formed on the xylem side than on the phloem side.

The cells formed from the cambium in the region of the pith rays become pith-ray cells. The activity of the cambium thus increases the length of the pith rays, so that the bundles and pith rays grow equally.

The formation of new cells from the cambium results in an enlargement of the stem that is known as the secondary thickening. The formation of new cells



in secondary thickening continues throughout the life of the plant. It is in this way that the trunks of trees continue to grow in diameter.

After the cells which are to form xylem or phloëm are cut off from the cambium, they undergo one or more tangential divisions before being differentiated into permanent tissue. In this way the cambium frequently comes to be bordered on both sides by cells which are very similar in appearance to cambium cells. The result is that on superficial observation the cambium appears to be several cells thick.

**Bast fibers.** In the secondary phloëm there is very frequently an alternation of bands of thick-walled sclerenchyma fibers (known as bast fibers) and bands of thin-walled phloëm cells (Figs. 139, 140). The bast fibers are like other sclerenchyma cells in being elongated, pointed, thick-walled dead cells whose function is to give strength to the group of tissues in which they occur. The term *bast fiber* is frequently used in a collective sense to denote the sclerenchyma fibers of the cortex, the pericycle, and the phloëm. Strands of bast fibers have long been used by man for industrial purposes, having furnished early savages with bowstrings and material for cloth. Among the

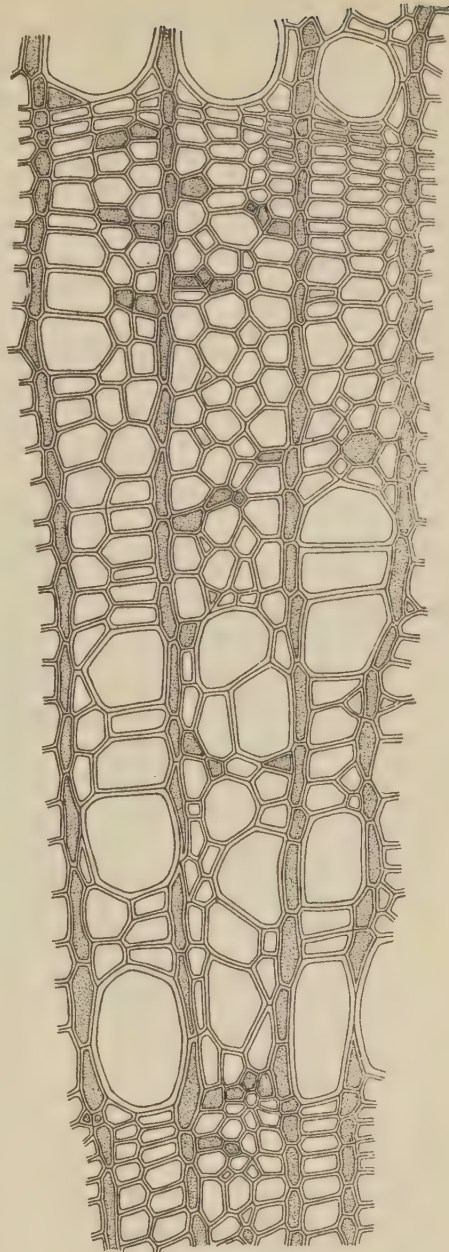


FIG. 141. Cross section of the secondary wood of a linden stem

Rows of cells extending from top to bottom, pith rays; large, thick-walled openings, vessels; smaller empty cells, wood fibers; small cells with gray contents, wood parenchyma. An annual ring ends with the small cells in the lower part of the drawing; another begins with the large vessels and ends near the top, just below the large vessels of the succeeding ring. ( $\times 255$ )

best-known commercial bast fibers are flax (from which linen cloth is made), hemp, jute (much used in making coarse sacks), and ramie (the so-called China grass).

**Annual rings.** In regions with a very pronounced cold season the diameter growth of woody plants takes place only during the spring and summer, and not in the winter. The wood of



FIG. 142. Cross section of a three-year-old linden stem

In the center is the pith surrounded by three annual rings of wood. In the bark are alternating strands of phloem and bast fibers

one season is sharply marked off from that of the next, because the wood formed first consists more largely of vessels than does that formed later, when wood fibers are relatively more abundant (Figs. 141, 142). In many trees, vessels are formed only or largely in the first part of the season's growth. The production of the vessels early in the season is advantageous to trees in several respects, and is connected with their seasonal activities.

In actively growing trees the number of leaves increases each year, and as all the foliage for a year is expanded during the early part of the growing season, additional vessels are needed at that time to supply the increased foliage. Moreover, the vessels in the leaves formed during one season are directly connected with the wood produced that same season; so, for this reason also, it is advantageous for the vessels to be formed as soon as possible, even when, as in trees past their prime, there is no increase in the number of leaves. In the case of coniferous trees similar conditions obtain, and the tracheids



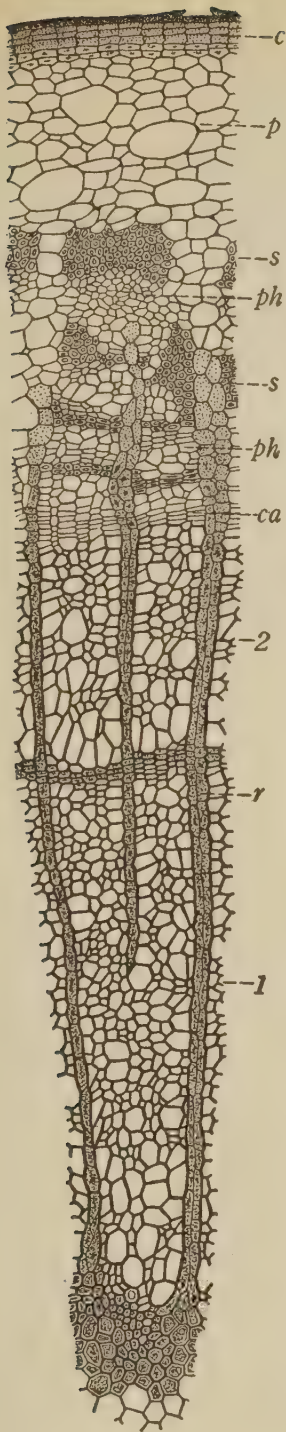


FIG. 143. Cross section of a portion of a two-year-old stem of tulip tree (*Liriodendron tulipifera*)

Near each side is a primary pith ray, while in the center is a secondary ray. 1, first annual ring of wood; 2, second annual ring of wood; *r*, pith ray; *ca*, cambium; *ph*, phloëm; *s*, bast fibers; *p*, parenchyma; *c*, cork. ( $\times 65$ )

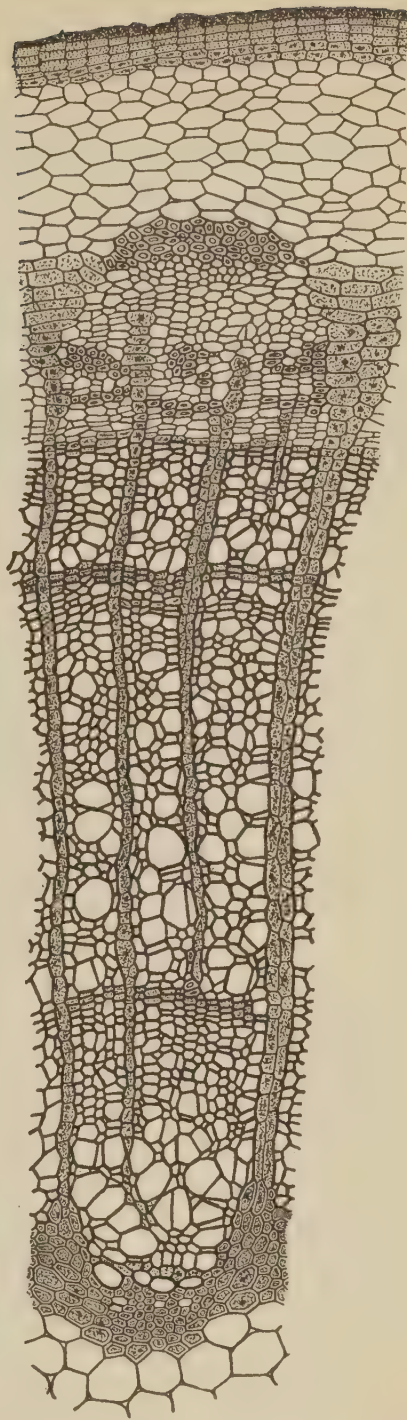


FIG. 144. Cross section of a portion of a three-year-old stem of tulip tree (*Liriodendron tulipifera*) with three annual rings of wood

Notice the primary, secondary, and tertiary pith rays. ( $\times 75$ )

formed in the spring are much larger than those produced in the latter part of the growing season (Fig. 130). It is thus easy to distinguish the rings of wood formed in successive years in

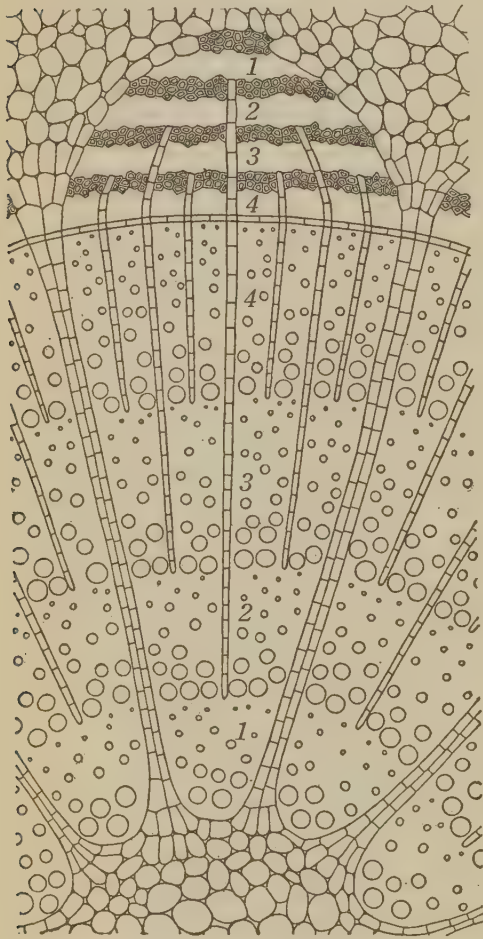


FIG. 145. Diagram of secondary thickening in a vascular bundle, showing four annual rings, labeled 1, 2, 3, and 4, in xylem and phloem

On both sides of the bundle pith rays run from the pith, while progressively shorter and shorter rays are found in the bundle. In the phloem region thick-walled sclerenchyma alternates with the phloem

continues, the outer edges of the xylem and the inner edges of the phloem in the bundles naturally become wider and wider. They do not increase in width very greatly, however, before

either dicotyledonous (Fig. 142) or coniferous trees of the temperate zones. These rings are called annual rings. The width of the annual rings varies with the environmental conditions at the time of their formation; during favorable seasons wider rings are produced than during unfavorable seasons. As each ring represents a single season's growth, the age of a tree can be determined by counting the annual rings. Fig. 143 shows a section of a portion of a two-year-old stem with two rings, while Fig. 144 represents a portion of a stem with three narrower rings. Similar rings are sometimes produced in tropical countries by the alternation of pronounced wet and dry seasons; in this case the fundamental physiological factors involved are essentially similar to those just described. In most trees growing in tropical countries, where there are no pronounced changes of season, there are no annual rings (Fig. 140).

**Secondary pith rays.** As the course of the secondary thickening



the cambium cells, which are at the center of the bundle, cease to form xylem and phloëm but give rise to pith-ray cells. In this way new pith rays are formed in the bundles (Figs. 140, 143-145). As the secondary pith rays do not extend to the central pith or to the outer edge of the phloëm, they are not as long as the primary rays. When the secondary thickening has progressed farther, tertiary pith rays make their appearance. They are naturally not as long as the secondary rays. In the same way, as thickening proceeds, other and progressively shorter pith rays are formed as is shown in Figs. 144 and 145.

The pith rays extend radially in the stem for considerable distances, the primary rays reaching from the pith into the bark; but the vertical extension is slight. The radial extension of the pith rays is of advantage, as they conduct food materials and water radially in the stem. A considerable vertical extension would offer no such advantage but would result in weak places where the stem could be rather easily split. The vertical extension of pith rays is seen very readily in tangential sections. Tangential sections are longitudinal sections perpendicular to the pith rays (Fig. 147).

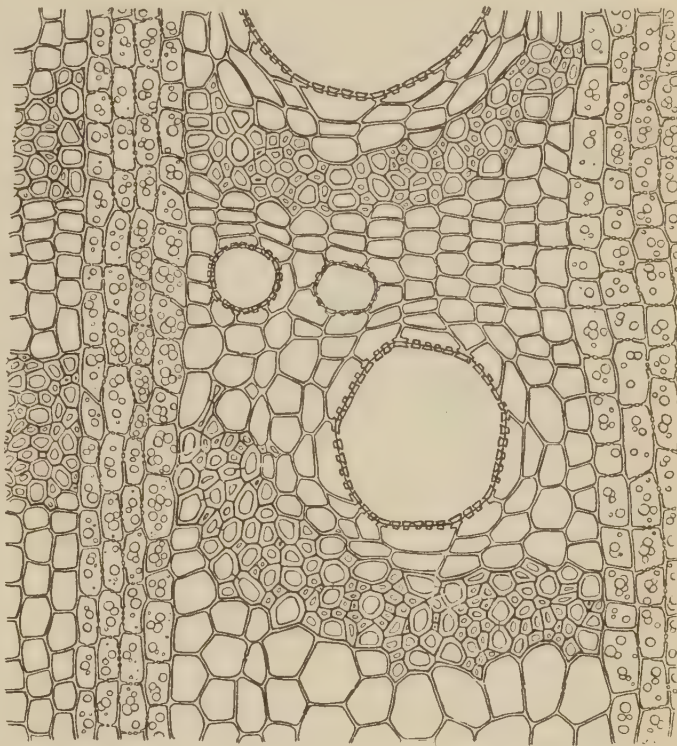


FIG. 146. Cross section of wood of coral tree (*Erythrina fusca*), a tree that has an unusually large amount of wood parenchyma and in which the wood parenchyma and wood fibers are exceptionally distinct

The rows of cells containing starch grains are pith rays, the small thick-walled cells are wood fibers, the small thin-walled cells between them are wood parenchyma, and the large openings are vessels. ( $\times 85$ )

**Heartwood and sapwood.** The wood of large tree trunks consists of an outer region known as *sapwood* and an inner portion, the *heartwood*. The sapwood is usually light in color and from about a centimeter to several centimeters in thickness. In the sapwood the parenchyma cells are alive, and so it is in this portion of the wood that food is stored. Also, the ascending

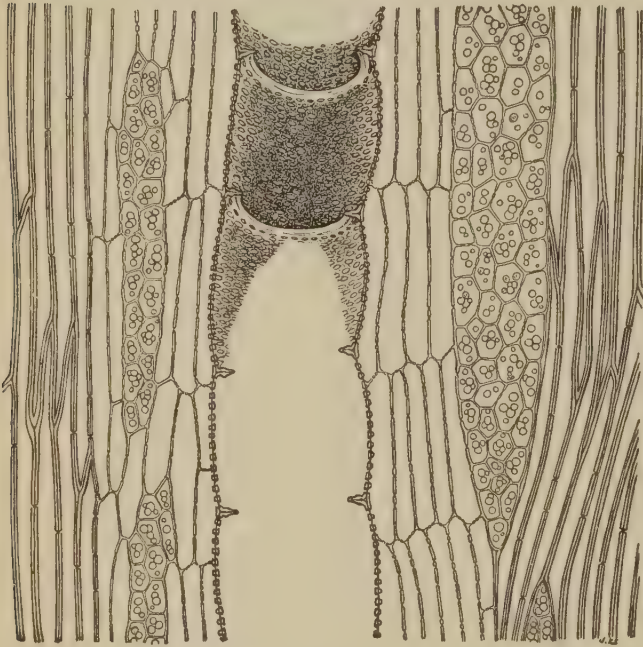


FIG. 147. Tangential section of wood of *Erythrina fusca*

A vessel is in the center, wood fibers with thick walls and pointed ends are at the sides, and the elongated, blunt-ended cells are wood parenchyma. The groups of cells containing starch grains are pith rays. ( $\times 75$ )

current of water moves in the sapwood, and not in the heartwood, which has practically no other function than that of mechanical support. The heartwood frequently has a darker color and is more resistant to decay than is the sapwood. Wood does not decay by itself, decay being due to the action of bacteria and fungi. The parenchyma cells of the heartwood are generally dead, but before they die they usually produce tannin, or some other antiseptic material, which permeates the walls of the neighboring cells. This antiseptic material makes the wood more resistant to the attacks of bacteria and fungi, and it is for this reason, and also because the heartwood contains less food material than the sapwood, that the heartwood is generally more resistant to decay and to the attacks of insects than is the sapwood. The dark color of the heartwood is also usually due to tannin, resins, or gums produced by the parenchyma cells.

**Weight of wood.** The variation in weight of woods is very great, as they contain varying quantities of air, but the wood



substance itself has approximately the same weight in all species, being about 1.6 times as heavy as water. Therefore all woods would sink if they did not contain a considerable amount of air in the dead cells and intercellular spaces. When this air is removed, as after long submergence in water, the wood sinks. From the above it follows that the weight of a given wood will depend on its density, that is, on the relative proportion of wood material and air. The density and weight naturally vary with the number of wood fibers and the thickness of their walls. Wood that contains a great deal of parenchyma and few fibers is light (Fig. 146), while wood composed largely of thick-walled fibers is heavy.

**Fuel value of wood.** The fuel value of wood varies with its weight, as equal weights of wood produce equal quantities of heat. In general it may be said of woods otherwise equal that those light in weight kindle easily and flash quickly, the fire spreading rapidly, while those that are heavy behave in the opposite way.

The longitudinal arrangement of the fibers of wood explains why it is much easier to split it longitudinally than to cut across it. Wood splits most easily along the radii, on account of the radial arrangement of the pith rays.

**Wood pulp.** Paper made from wood consists essentially of the fibrous elements, which are separated and then pressed together into sheets. In making paper from wood the fibers are

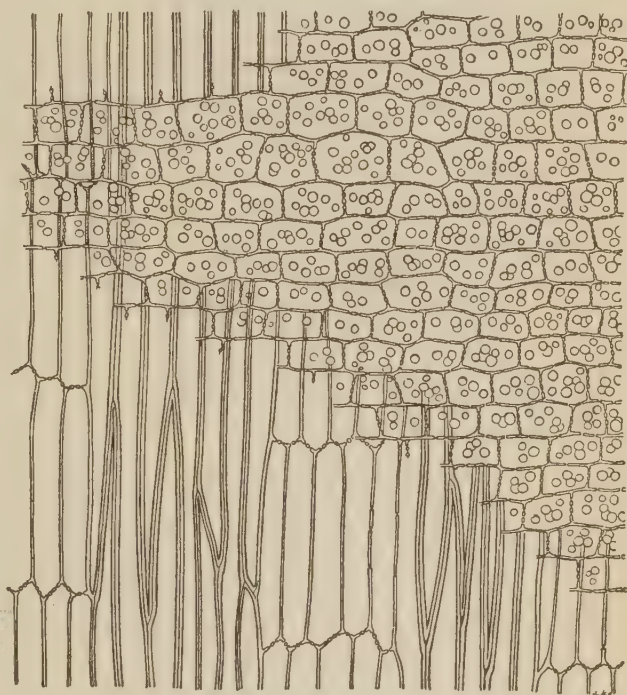


FIG. 148. Radial section of wood of coral tree (*Erythrina fusca*)

The wood fibers and wood parenchyma have the same characteristics as in the tangential section (Fig. 147). The group of cells containing starch grains is part of a pith ray. (× 95)

separated, either by mechanical grinding or by boiling with chemicals. The loose fibrous material that is obtained in either of these ways is known as wood pulp. While wet, this pulp is combined with resin, clay, or other materials to give body and added strength, after which the pulp is pressed into paper.

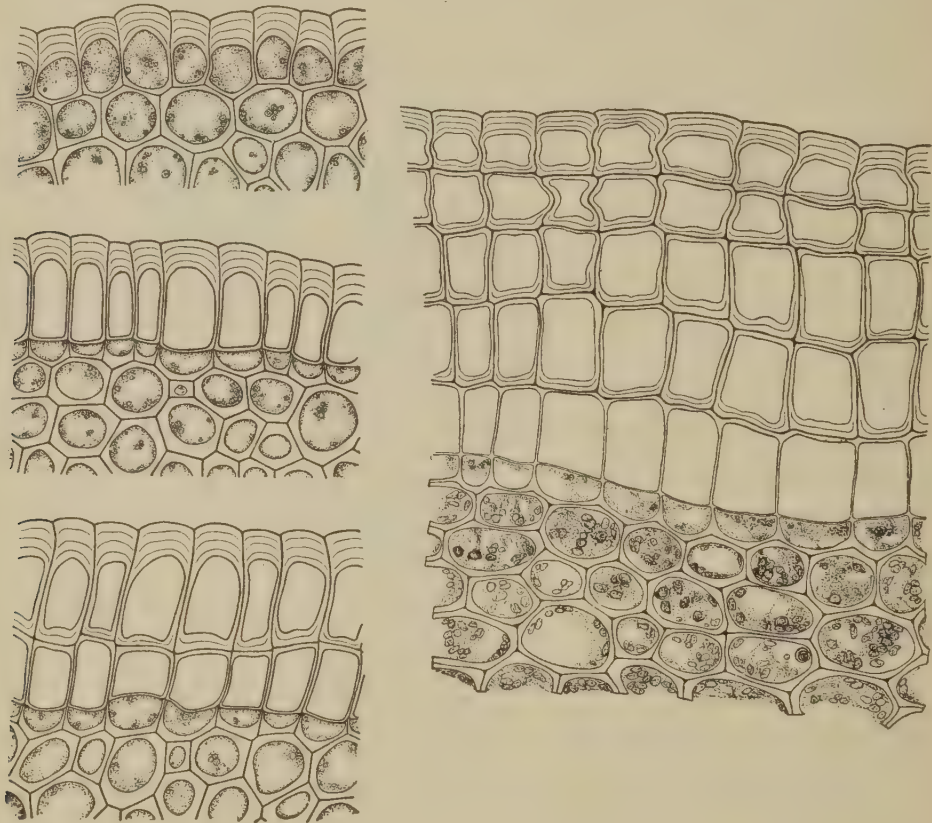


FIG. 149. Stages in the formation of cork of oleander (*Nerium oleander*)

Upper left, epidermis and outer part of cortex before the formation of a phellogen layer. Left center, the epidermal cells have elongated and divided to form a row of epidermal cells and below this the phellogen layer. Lower left, the phellogen layer has produced a single row of cork cells between the epidermis and the phellogen. Right, the uppermost row of cells is the epidermis, the next four rows are cork, while the sixth row from the top is phellogen. ( $\times 250$ )

**Secondary changes in the bark.** As the wood of the stem is enlarged by the cambial activity there is a tendency for the regions outside of the younger phloëm to be stretched. This is partly compensated for by radial divisions of the parenchyma cells. When, however, there is a band of sclerenchyma, such as occurs in the pericycle of some stems (Fig. 113), the dead



sclerenchyma cells cannot grow and divide, and can be stretched but little, if at all. Therefore, as the wood increases in diameter the band of sclerenchyma is ruptured and parenchyma cells are pressed in between the isolated strands formed by the breaking up of this sclerenchyma ring.

The epidermis frequently increases in size by radial growth and division, but it seldom happens that the epidermis grows fast enough to prevent it from being ruptured by the increase in size of the tissues within it. If the place of the epidermis were not taken by some other protecting tissue, the cracking of the epidermis would expose the underlying tissue to an excessive rate of evaporation and would also allow the entrance of disease-producing organisms. These contingencies are prevented by the formation of cork.

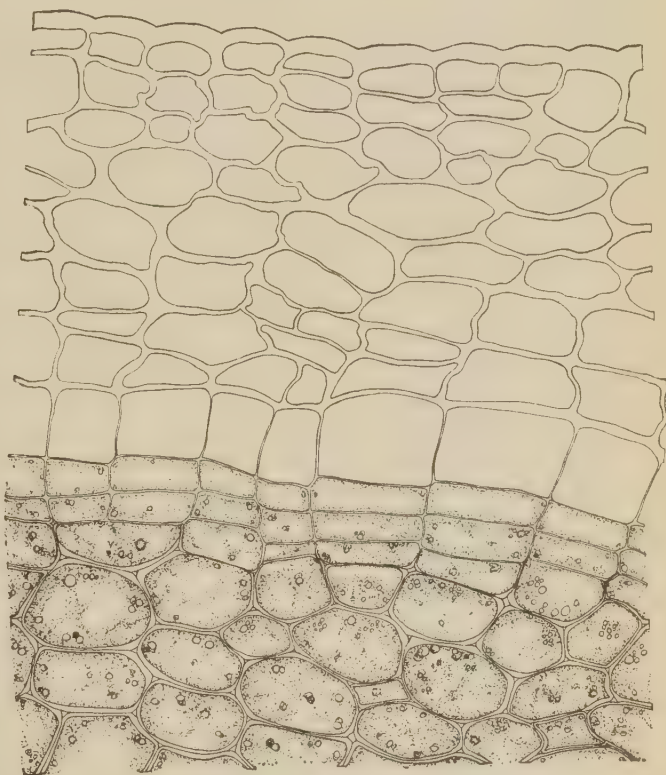


FIG. 150. Early stage of cork formation in *Ixora finlaysoniana*. ( $\times 250$ )

**Cork.** Cork consists of dead cells which fit close together without intercellular spaces (Fig. 149). The walls of cork cells are impregnated with a waxy substance, suberin, which makes them practically impervious to water. Cork is familiar in the form of ordinary cork stoppers, which are obtained from the cork oak of Spain, on which cork is exceptionally well developed. Cork not only restricts transpiration but, like the epidermis which it replaces, hinders the entrance of parasites and affords mechanical protection.

**Phellogen.** The cork is formed from a layer of secondary meristem known as the *phellogen*. In stems the first phellogen

usually arises in the outermost layer of the cortex or in the epidermis (Fig. 149) by a tangential division of the cells, but it may have its origin in a deeper layer (Fig. 150).

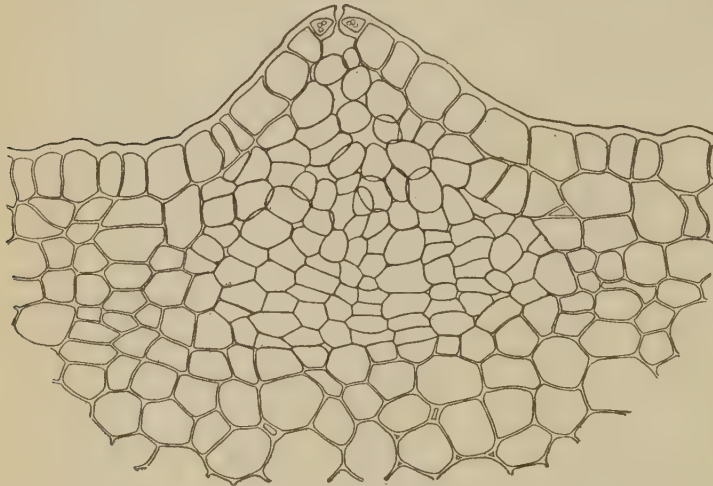


FIG. 151. Beginning of lenticel formation under a stoma of mulberry (*Morus alba*). ( $\times 230$ )

When the phellogen is formed by tangential division of the epidermis, the outer layer of cells remains epidermal, while the inner becomes the phellogen. When the outermost layer of the cortex by tangential division gives rise to the phellogen, it is the outer layer that becomes phellogen. As the phellogen is formed by the division of cells which had previously lost all the characteristics of meristematic cells, it is called secondary meristem. After the phellogen layer is formed,

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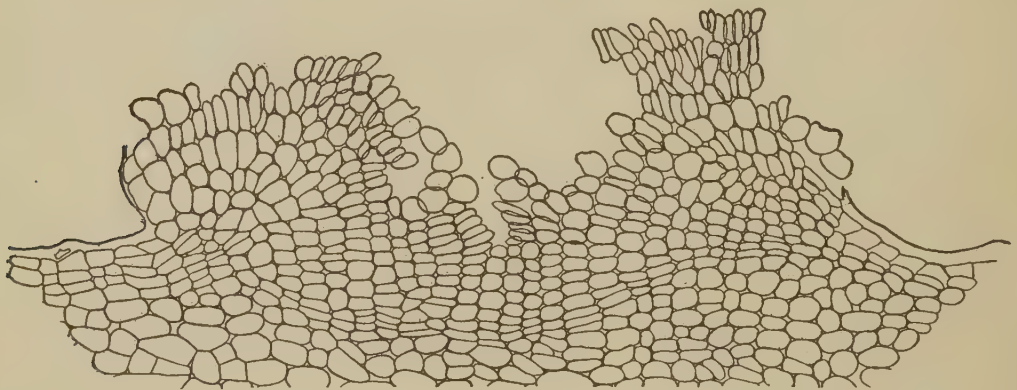


FIG. 152. Lenticel of mango (*Mangifera indica*)

Note the phellogen layer extending under the lenticel. ( $\times 95$ )

it divides tangentially and gives rise to radial rows of cork cells toward the exterior (Fig. 149) of the stem, and frequently to parenchyma cells toward the interior. The cork cells soon become suberized and die. Also, the cutting off of the water supply



of the cells that are exterior to the cork results in their death, and after a time they peel off and disappear.

The first-formed phellogen does not function indefinitely but is replaced by another, produced in the underlying tissue. The second phellogen is likewise replaced by a third, and so on until the phellogen may come to be formed in the secondary phloëm. As the older parts of the bark tend to peel off, the bark of old trees may consist only of secondary tissues, the cortex, pericycle, and primary phloëm having been shed.

**Lenticels.** Stomata allow for an exchange of gases through an epidermis, and in the same way the lenticels allow for an exchange of gases through the cork. Lenticels are formed under the stomata

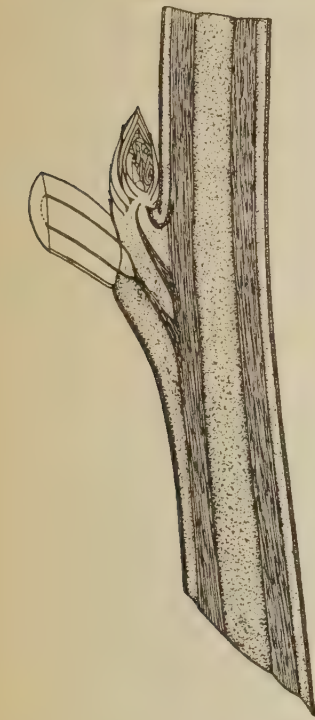


FIG. 153. Abscission layer at base of a mulberry leaf (*Morus alba*).  
( $\times 1$ )

(Fig. 151) and consist of radial rows of cells with intercellular spaces (Fig. 152). Like the cork cells they are formed from the phellogen. The intercellular spaces allow for an exchange of gases.

**Leaf fall.** The fall of leaves is brought about by meristematic activity of cells across the base of the petiole. These produce layers of parenchyma cells which separate and cause the leaves to fall (Fig. 153). The scars are protected by lignification and suberization of the exposed cells and by the formation of a layer of cork continuous with that which covers the stem.

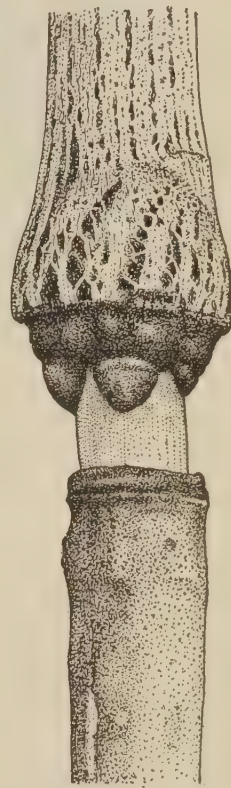


FIG. 154. A girdled tree trunk, showing greater growth above than below the wound

**Healing of wounds.** When a cut is made into the wood of a dicotyledon or a conifer, the cambium cells adjoining the wound area proliferate and produce what is known as a callus. This grows over the wound and covers it (Fig. 155). A phellogen layer is produced in the outer part of the callus, while a cambium, which is continuous with that in the stem, is formed in the interior. As the edges of the callus grow together over the wound the edges of the cambium also coalesce.

Removal of a strip of bark and cambium all the way around the trunk of a tree is called girdling. If the strip removed is

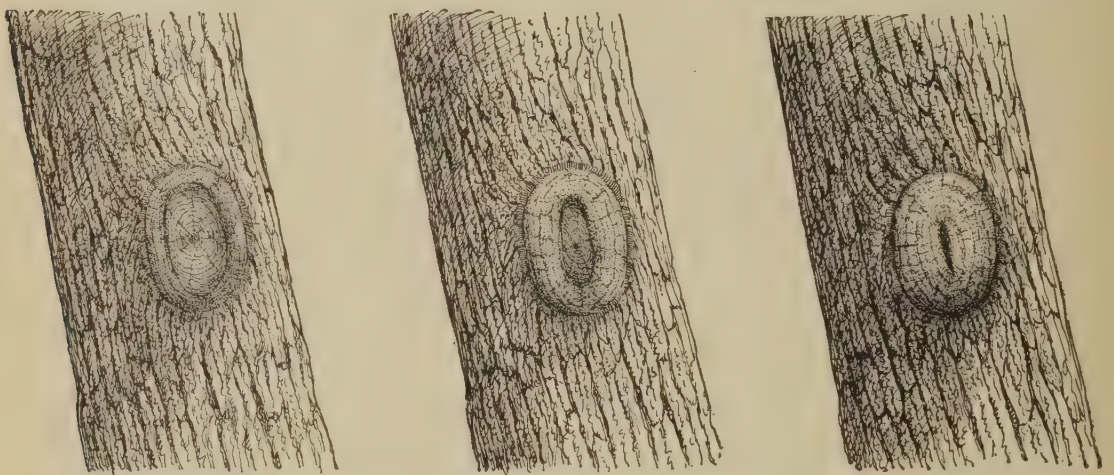


FIG. 155. Stages in healing of wound caused by removal of branch

sufficiently wide, the tree will be killed, because this operation destroys the food-conducting tissues which supply the roots. Some plants will recover from girdling if the strip removed is not too wide, as the wound may heal by the production of a callus and the subsequent formation of new conducting tissues. When a tree is girdled, the part of the trunk above the wound grows much faster and produces a much larger callus than that below it (Fig. 154), as the part above the wound is abundantly supplied with food material, while the part below is not.

**Pruning.** In trimming a tree, branches should be cut off even with the trunk, and no portion of a dead or amputated branch should be left if the wound is to heal properly. Stumps of branches are not in the direct line of the movement of food materials and usually die quickly if they do not send out new



shoots. A callus formed from the main stem then starts to grow out over the stump, but before the stump is covered it begins to decay, as is clearly illustrated in Fig. 156. The decay extends into the wood of the main branch and trunk, with the result that the tree becomes hollow. For similar reasons, if a twig is to be cut back but not removed, the cut should be made a little above a bud and not in the middle or upper part of an internode. If a portion of an internode is left, it dies and its presence interferes with the closing of the callus over the wound.

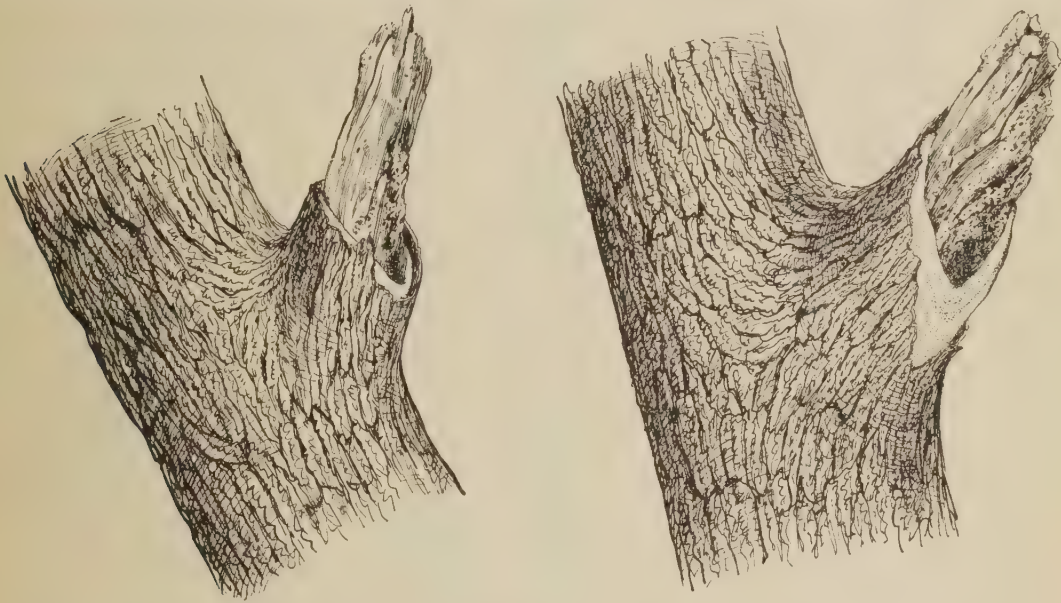


FIG. 156. Dead stumps, showing how decay may enter a tree trunk

**Budding and grafting.** Budding and grafting consist in inserting a part of one plant into another in such a way that a permanent union is formed and the inserted piece continues to grow. The part which is inserted is known as the *scion*, and the plant into which it is inserted is called the *stock*. The success of the operation depends primarily upon bringing the cambium of the scion into contact with that of the stock.

*Budding* consists essentially in removing a small piece of bark with a bud and little or no wood from one plant and inserting it under the bark of another plant (Fig. 157). The piece inserted is known as the *bud*. The usual method is called shield budding, on account of the shieldlike shape of the bud. In this method an oval piece of bark with a bud is cut from one twig.

The stock is usually cut off above the place where the bud is to be inserted, while at the place of insertion a T-shaped slit is made through the bark into the cambium. The flaps are then loosened and the bud is inserted under them. The preparation is bound tightly to insure close contact of the inner surface of the bud with the cambium of the stock and to prevent the bud

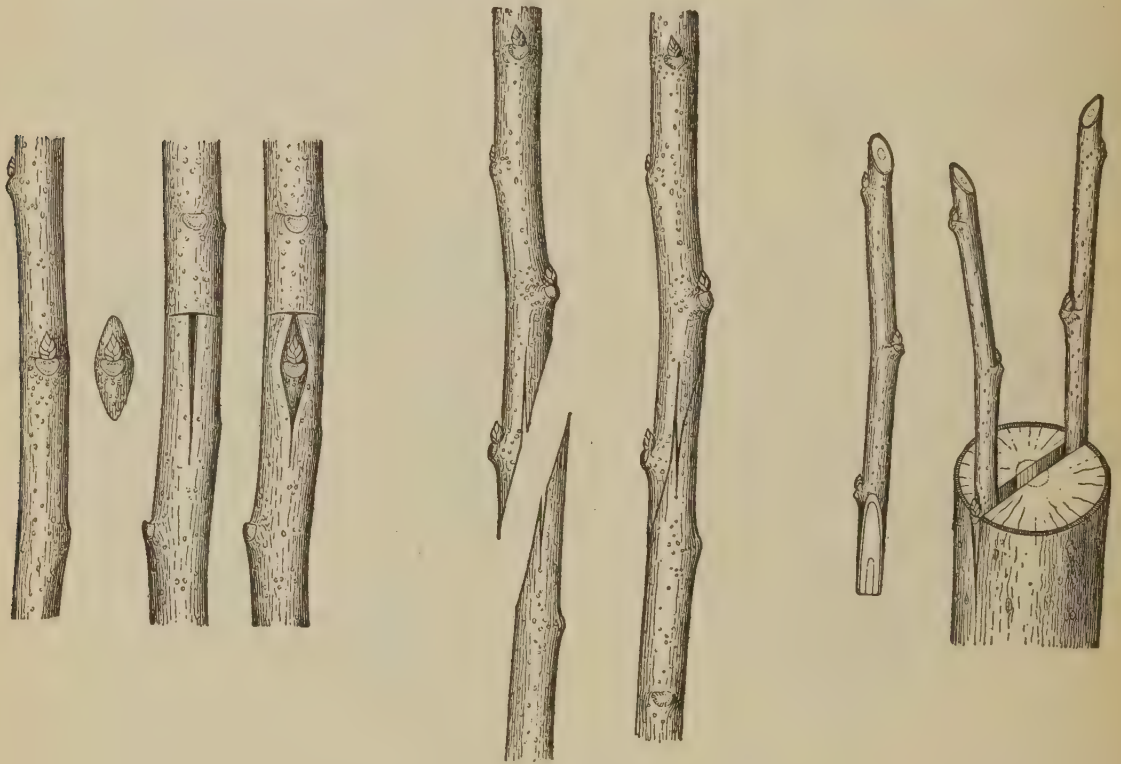


FIG. 157. Budding and grafting

Left, budding ; center, whip grafting ; right, cleft grafting

from getting out of place. The junction should then be very carefully sealed with grafting wax to prevent loss of moisture.

*Grafting* consists in cutting off a piece of stem of one plant and inserting it into another. The common method of grafting when the stock is large is known as *cleft grafting* (Fig. 157). The scion consists of a small piece of twig with several buds. Its base is cut like a wedge. A vertical cleft is made into the decapitated stock and the scion inserted so that its cambium comes in contact with that of the stock. The wound is covered with wax to prevent drying. *Whip grafting* is employed on small stocks. In this method both stock and scion are cut



obliquely and a vertical cleft is made in each. Stock and scion are then fitted into each other so that the cambiums are in contact. They are then tied together and the junction is sealed with wax.

### GROWTH

The growth of a plant is usually accompanied by the addition of new material, but growth may consist in the rearrangement of materials already present. The latter is evidently the case when a potato or an onion sprouts in a dry, dark place, as under these conditions it is impossible for a plant to absorb water or mineral matter or to carry on photosynthesis. Growth in such cases is accompanied by an actual loss in weight, due to the breaking down of compounds in the process of respiration. This is necessary for the release of the energy used in the rearrangement of the materials taking part in the new growth.

**Grand period of growth.** If the formation and growth of a plant organ or a limited part of a plant are considered, it will be found that during its formation the rate of growth is slow. As it becomes older it grows more rapidly up to a certain period, and then more and more slowly until it is mature and growth ends. The total growing period is known as the *grand period of growth*. It can be divided arbitrarily into three stages, or phases, which necessarily overlap. The first is the phase of *formation*, during which the organ or other limited part of the plant has its initiation. The chief activity during this period consists in the multiplication of cells, and the rate of growth is relatively slow. Before the cells have ceased to divide, the part concerned enters into the next phase, that of *enlargement*, during which the cells enlarge and approach their mature size. This enlargement takes place with relative rapidity, and any part of a plant makes its most rapid growth while in this phase. After the cells have reached approximately their mature size, they enter the phase of *maturation*, during which they assume their mature characteristics. A part of a plant in this phase grows slowly, as the cells have, to a great extent, ceased enlarging.

## EFFECT OF EXTERNAL FACTORS ON GROWTH

**Water.** An abundant supply of water is very essential to the most rapid growth of plants. It is a well-recognized fact that plants which lack water grow more slowly and produce smaller quantities of dry material than do plants that are abundantly supplied with water.

Any part of a plant, in order to grow, must contain enough water to be turgid. When cells or plant organs lose their turgidity, they decrease in size. Leaves, fruits, or stems may lose more water on a dry, sunny day than they absorb, and actually become smaller than they were during the preceding night. It is therefore necessary for normal growth that a plant should be able to obtain not only enough water to replace that which is lost through transpiration but, in addition, enough to fill the newly formed tissue. The amount needed for growth is very small as compared with that lost through transpiration.

The actual rate of transpiration is not so important as is the ratio between water lost and water absorbed. It is highly important that the daily rates of transpiration and of water absorption should be so balanced that the water absorbed is sufficient to replace that lost by transpiration and to support new growth. Excess of water loss over water absorption may be brought about either by a high rate of evaporation or by a low moisture content of the soil, or by a combination of these two. This condition can usually be remedied by either decreasing the rate of evaporation or increasing the water content of the soil. In agriculture the method most generally practiced is to supply water, as by irrigation.

**Heat.** At very low temperatures plants do not grow. The minimum, or lowest, temperature at which a plant will grow varies with different species, but 4° C. may be regarded as an average minimum temperature for many plants. As the temperature increases beyond the minimum the rate of growth becomes more rapid until the optimum temperature is reached. This optimum temperature also varies with different species, but



probably averages from 28° to 30° C. If the temperature rises beyond the optimum, the rate of growth decreases until a temperature is reached above which no growth takes place. This temperature is known as the maximum. The minimum and the optimum temperatures for growth vary not only with different species but also with changes in other environmental conditions.

The effect of temperature is not confined to the direct action of favorable or unfavorable temperature on the rate of growth. Thus, trees from the temperate zone do not thrive in the tropics, where the temperatures are favorable to growth throughout the year. Trees which are native to the temperate zone seem to need a winter season, while tropical ones do not.

Trees and shrubs of the temperate zone, which are usually

dormant during the long winter, tend to become dormant in the tropics after a period of activity. Unless they are exposed to an extensive period of cold though not necessarily freezing weather, the resumption of growth is greatly delayed, while the growth is lacking in vigor (Fig. 158). It is probably for this reason that such fruits of the temperate zone as apples, pears, peaches, and cherries do not thrive in the tropics. They grow well for a time and then become half dormant and, in the absence of chilling, never fully recover from this condition.



FIG. 158. Photographs of blueberry twigs, both taken in the spring at the same time

The one on the left had been exposed to a cold winter while the other had been kept warm in a greenhouse  
(After Coville)

The advantages of chilling for trees of the temperate zone seem to be connected with changes in the character of the stored food. During the summer and autumn food is stored in the form of starch, which is insoluble. Before this can be used for growth it must be changed to sugar, which is soluble, and in these plants this change appears to take place most readily at low temperatures.



FIG. 159. Effect of lengths of day on different types of plants

Left, *Helianthus angustifolius*, a "short-day plant." Both specimens planted March 2 and photographed July 31. Plant at left kept in the dark during a portion of each day and exposed to light for only ten hours. Plant at right exposed to light for full length of day. Right, red clover, a "long-day plant," photographed June 28. Plants at left kept in the dark during a portion of each day and exposed to light for only ten hours. They assumed a prostrate form of growth and were greatly delayed in flowering. Plants at right exposed to light for full length of day during spring and early summer. (From work of Garner and Allard, Bureau of Plant Industry, United States Department of Agriculture)

Trees of the temperate zone are afforded valuable protection by the fact that in the fall they enter into a condition of dormancy from which they do not emerge until exposed to prolonged chilling. If such plants were so constituted as to start into growth as easily in the warm days of late fall as they do in early spring, many species would come into flower and leaf in warm autumn days which follow cold ones, and the stored food that they require for their normal vigorous growth in the following spring would be wasted in the growth of new twigs



which would be killed by the first heavy freeze. These evil results are prevented when two or three months of chilling are necessary before a dormant plant will respond to a favorable temperature by the resumption of growth.

**Light.** As the growth of green plants is dependent on photosynthesis, plants cannot continue to grow for any great length of time without light. On the other hand, high light intensities are usually accompanied by rapid rates of evaporation. In the preceding chapter it was pointed out that plants may contain less water on sunny days than on cloudy days or during the night. This condition frequently results in a much more rapid rate of growth during the night than during the day, and plants may even cease growing or actually shrink during bright, dry days.

The relative length of day and night is a very important factor in determining the fruiting season of plants. Some plants, as poinsettia (Fig. 80), will flower and fruit only during seasons with short days, and others only when the days are long. In temperate zones the days are long during the summer, shorter in autumn, and still shorter in winter. It has been found that many plants which normally do not flower until the short days of autumn can be made to bloom during the long days of summer if they are placed in the dark for a portion of each day (Fig. 159). Also, many plants that usually blossom in the summer and not in the winter, even if in a heated greenhouse, will produce flowers during the short days of winter if kept in a warm greenhouse and illuminated by electric lights for a portion of each night (Fig. 159).

While the period of flowering may be hastened by shortening the daily exposure to light, the rate of growth frequently



FIG. 160. Fasciated stem of cockscomb

increases with the length of the daily exposure. When plants which germinate in the spring and flower in the fall are forced into bloom early in the summer by shortening the daily exposure to light, they are small at the time of flowering.

In the tropics the days are always shorter than the summer days of temperate zones. Plants from the tropics may fail to flower during the long days of northern summers and produce

flowers and fruits abundantly in greenhouses during the shorter days of winter.

The fact that the days are shorter in the tropics than they are during the summer in temperate zones may explain why many of the plants of the temperate zone do not succeed in the tropics.

**Abnormal forms of growth.** Stems and other plant organs frequently show abnormal growths. One of

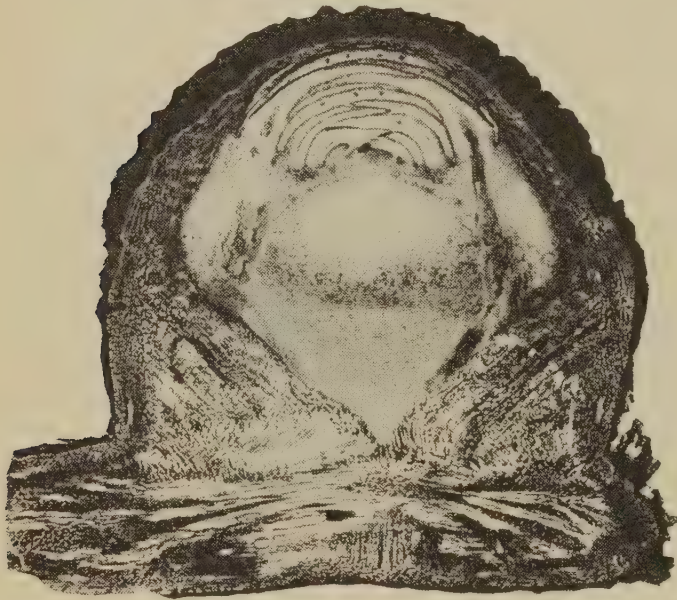


FIG. 161. Section of a gall on a *Cissus* root in which a bud of *Rafflesia manillana* is developing. Later the bud will burst through the gall. Compare with Fig. 7

the most common is a flattened form, called fasciation, which occurs when a stem has several growing points instead of a single one. This abnormality may be inherited, as in the cockscomb (Fig. 160), or it may be due to an injury, as by insects. Galls are another common class of abnormality. They may be produced by parasitic bacteria, fungi, flowering plants (Fig. 161), or various classes of animals, especially insects. Insect galls are very numerous, those produced by a given insect on the same kind of plant being constant in form. The mother insect lays its eggs in the host plant; and after the eggs hatch, the tissues of the plant proliferate and produce the galls.



## SPECIALIZED STEMS

The chief function of ordinary stems is to support the leaves and reproductive organs in such a way that they can carry on their several functions advantageously. Many stems, however, are specialized for functions which are unusual for stems, or are fitted to perform the usual functions in a somewhat specialized manner. Stems of these types may be called specialized stems. They may be divided into the following general classes: *unusual methods of support* (stem function), *photosynthesis* (leaf function), *absorption* (root function), *reproduction* (seed function), *storage*, and *protection*. This list is very similar to that given for specialized leaves. Frequently the only way in which we can tell by superficial examination whether a given structure is a stem or a leaf is by the mode of its attachment. If the structure is in the axil of a leaf, we regard it as a stem, while if a stem or bud is found in its axil, it is considered a leaf.



FIG. 162. Stems modified as hooks  
Above, *Artabotrys uncinatus*; below, *Uncaria gambier*. ( $\times \frac{1}{3}$ )

**Unusual methods of support (stem function).** Stems that are specialized in no other way than to support the leaves and reproductive organs in a rather unusual manner are well exemplified in climbing plants. The chief advantage of the climbing habit seems to be that it enables a plant to reach up into the



FIG. 163. Branches of *Bougainvillea* modified as spines used in climbing. ( $\times \frac{2}{3}$ )

light and bear large numbers of leaves without the necessity of expending the material which would be necessary to build a stem sufficiently strong to support the leaves and reproductive organs by its own strength. A climbing plant depends on the strength of some other object for its support, and so can develop long, slender stems. It is probably because of their slender stems that climb-

ers usually grow rapidly and so can shoot up through dense vegetation and reach the light more quickly than can a plant which has to develop a stem thick enough to support itself.

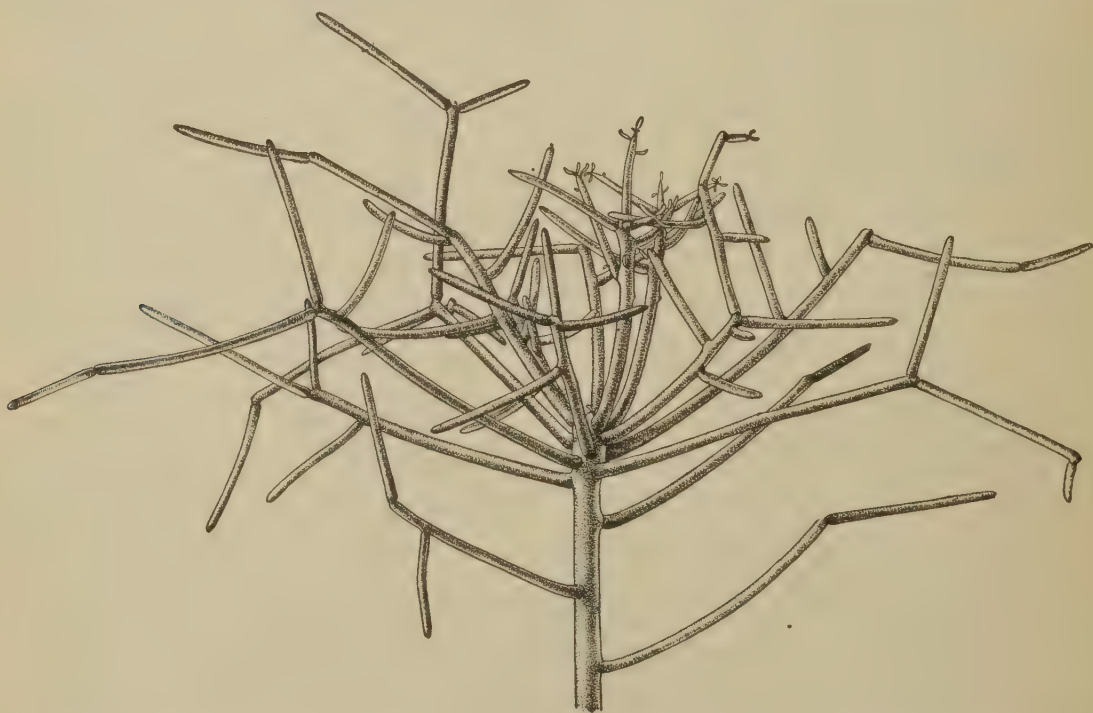


FIG. 164. Stems of *Euphorbia tirucalli* specialized for photosynthesis and water storage. ( $\times \frac{1}{3}$ )





FIG. 165. Stems modified as tendrils

Above, *Guania microcarpa*; left, *Antigonon leptopus*; lower right, *Cardiospermum halicacabum*. ( $\times \frac{1}{3}$ )



FIG. 166. Tendril of squash (*Cucurbita maxima*). ( $\times \frac{1}{3}$ )

The climbing habit has the disadvantage that the climbers are likely to fall with the death and decay of the plants on which they grow. Frequently they grow over and shade the supporting plant to such an extent as to kill it, and thus are instrumental in bringing themselves to the ground.

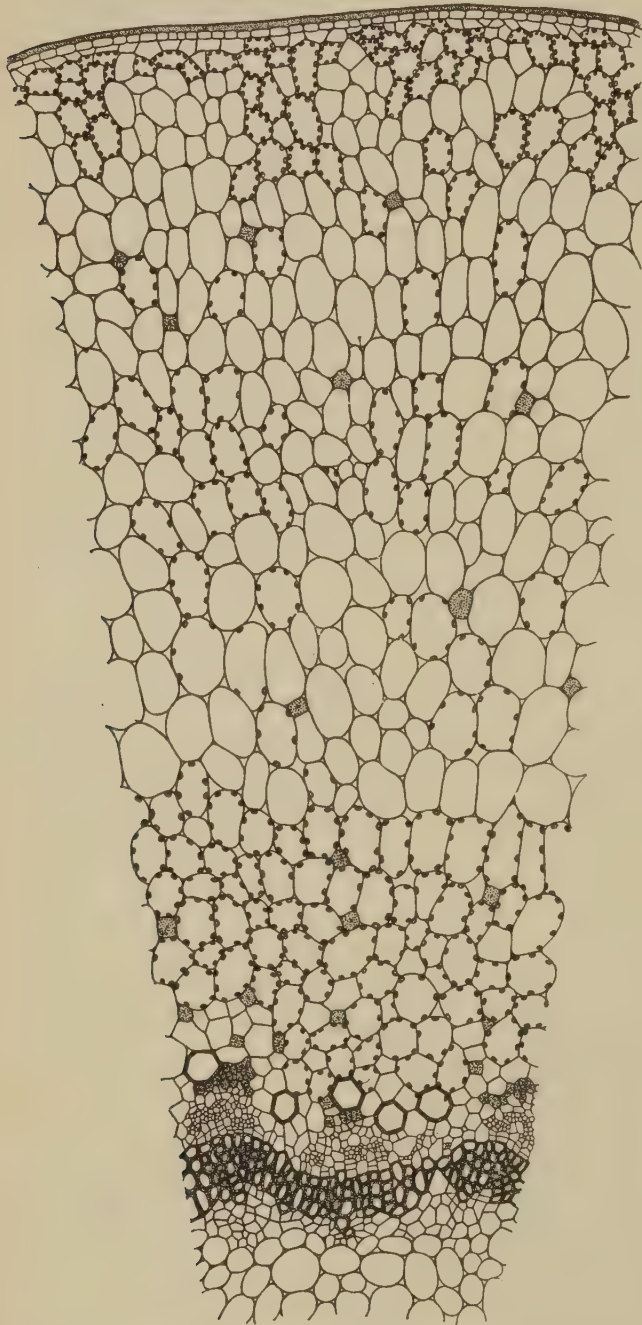


FIG. 167. Cross section of a portion of round stem of *Euphorbia tirucalli* (see Fig. 164)

Note the wide cortex specialized for water storage and photosynthesis

In order to utilize the strength of some other object a plant must have some means of attaching itself to its support. There are four general types of climbers: *twiners*, *tendrils*, *root climbers*, and *scramblers*.

**Twiners.** These plants climb by the simple device of twining spirally around a support. In nature such a support would be another plant. When twiners are cultivated, a wire cord or slender pole is usually substituted for the supporting plant. The morning-glory is a common example of the twiners.

**Tendrils.** Climbers belonging to this class are held up by tendrils which are either modified stems (Fig. 165) or



leaves (Fig. 69) or are of doubtful homology, as in the squash family (Fig. 166). Tendrils are long, slender structures which coil around other objects or, more rarely, bear disks which adhere to the surface of the support.

**Root climbers.** Many climbers adhere to a support by means of numerous small roots which develop from the stem (Fig. 179).

**Scramblers.** Climbers of this type are not so definitely fastened to their support as are those of the other types. They are held up more loosely by means of thorns (Fig. 163) or hooks (Fig. 162). Climbing roses and raspberries are examples of thorn scramblers. Hooks are more advantageous than thorns, as they have a greater tendency to keep a plant from slipping backward. The thorns or hooks may be stem (Figs. 162, 163) or leaf structures. Rattans are excellent examples of scramblers with hooks on the leaves (Fig. 70).

**Photosynthesis (leaf function).**

The young stems of green plants contain chlorophyll and carry on photosynthesis to some extent, while herbaceous stems continue to perform this function as long as they live. All green stems, therefore, perform to some extent the function which is the

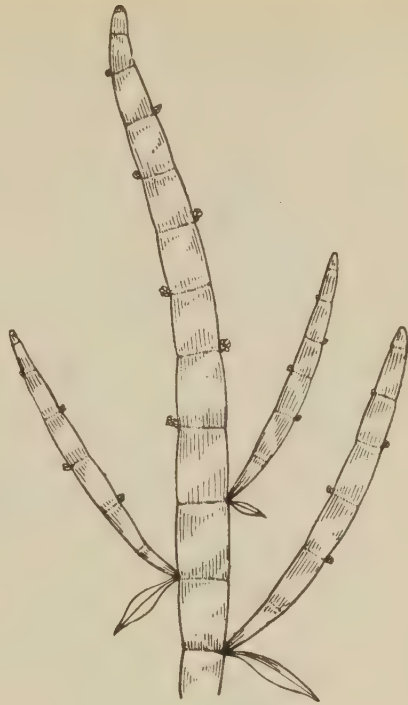


FIG. 168. Flattened stem of *Muehlenbeckia platyclada* specialized for photosynthesis. ( $\times \frac{1}{2}$ )



FIG. 169. Leaflike branches of *Phyllocladus protractus*. ( $\times \frac{2}{5}$ )

primary one of the leaf. In addition, numerous stems are specialized for photosynthesis and take the place of leaves in the manufacture of sugar.



FIG. 170. *Cuscuta*, a parasitic vine

The stems produce haustoria that enter the host and absorb water and food material. These haustoria are regarded as roots by some authorities. (× 1)

This is the case with the so-called asparagus fern and numerous sedges. Some stems which are specialized for photosynthesis are round (Figs. 43, 164, 167), others are flattened (Fig. 168), and others even have the form of leaves (Fig. 169). Such stems as those of the cacti (Figs. 512, 514) are specialized both for photosynthesis and for water storage.

**Absorption (root function).** The epidermal walls of submerged water plants are not cutinized; consequently both the leaves and the stems of such plants are capable of absorbing water and substances in solution in water.

The stems of some parasitic plants produce emergences which enter the tissues of the host and absorb water and food material (Figs. 170, 171).

The function of anchorage, which is one of the chief functions of roots, is performed to some extent by underground stems (Fig. 172), as in cannas and many grasses.



**Reproduction (seed function).** Many plants reproduce by means of stems (Fig. 5), this being by far the most usual mode of vegetative reproduction in flowering plants.

Two of the most common methods of stem reproduction are by *rhizomes* (stems that grow horizontally in the soil) and by *runners* (stems that grow along the surface of the soil). Both rhizomes and runners may produce roots at the nodes. In some species the internodes do not persist long, and each new node forms a new plant. In other species an increase in the number of plants comes about only by the branching of rhizomes and the ultimate decay of the whole of the older portion formed before branching took place (Fig. 172). The method of reproduction by runners, and especially by rhizomes, is well suited to increasing the number of plants in a limited area or to the invasion of an area next to that in which the parent plants are growing. A new plant growing from a rhizome has a much better

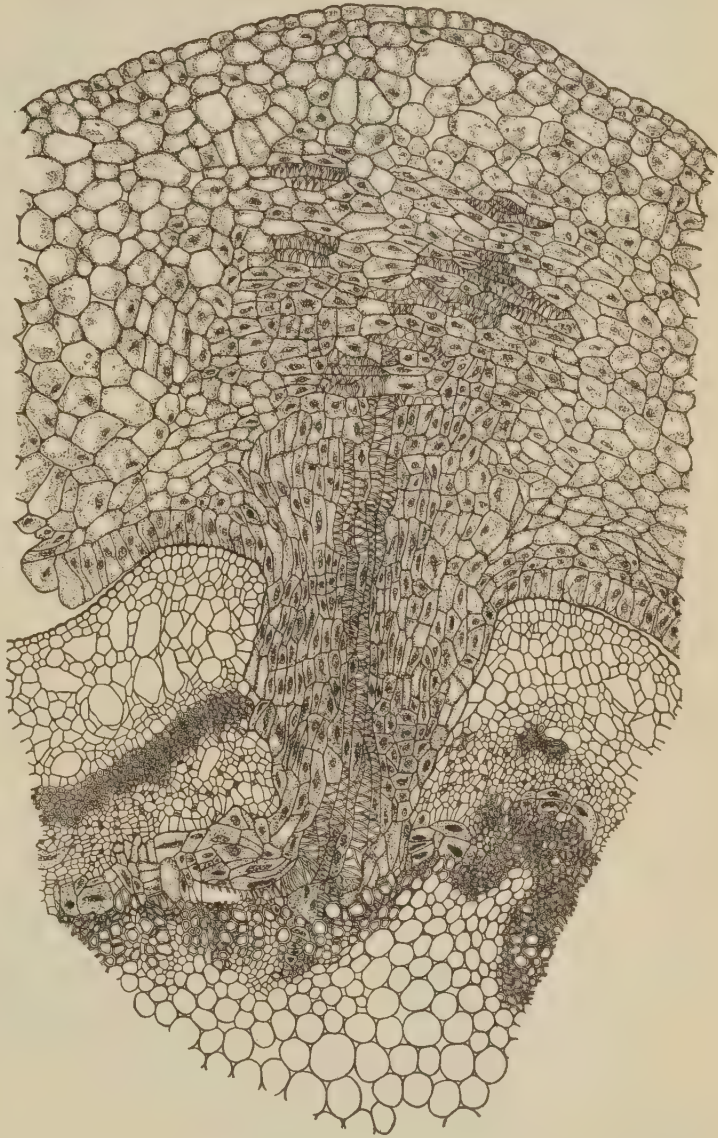


FIG. 171. Section through haustoria and portion of host of *Cuscuta* (see Fig. 170)

Note that cells of the haustorium are between the xylem and the phloem of the host, and that the xylem of the parasite is in contact with that of the host. ( $\times 70$ )

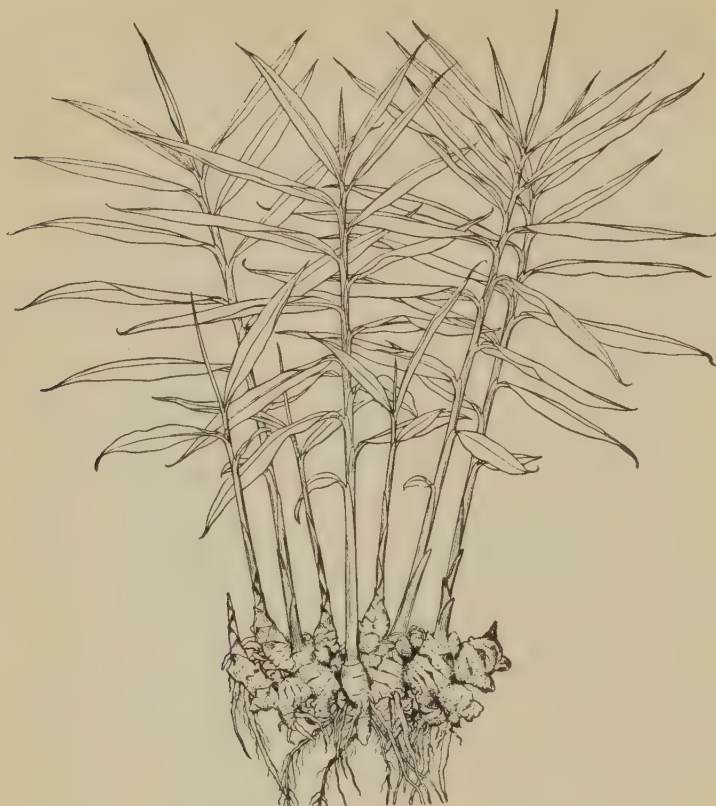


FIG. 172. Ginger plant with enlarged storage rhizome. ( $\times \frac{1}{7}$ )



FIG. 173. Storage rhizome of ginger. ( $\times \frac{2}{3}$ )

start than one growing from a seed, and, moreover, the rhizome is already in the ground, whereas the seed may never reach the soil.

Some stems grow up in the air at first and then, after they become long, bend down until they reach the ground, where they take root and so produce new plants.

**Storage.** Except when the roots or leaves are fleshy and especially modified for food storage the stem is usually the chief organ in which food is stored. In large plants, food is stored at certain seasons in considerable quantities in the pith rays and the wood parenchyma.

Some stems are especially modified for the storage of food. These are usually

underground stems such as the *rhizomes* of ginger (Figs. 172, 173), the *tubers* of potatoes (Fig. 174), or the *corms* of aroids (Fig. 175). While most stems that are specialized for food





FIG. 174. Tuber of potato  
( $\times \frac{2}{3}$ )

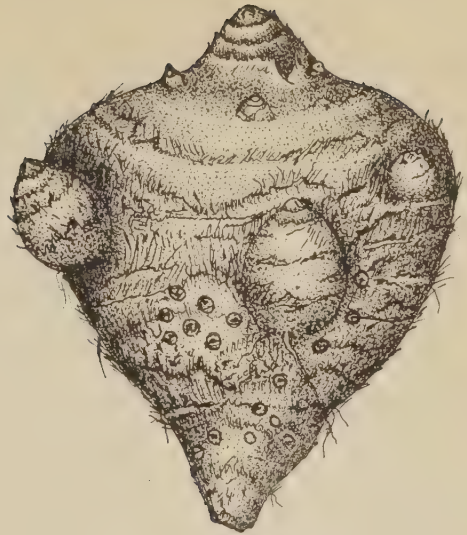


FIG. 175. Corm of taro (*Colocasia esculentum*). ( $\times \frac{2}{3}$ )

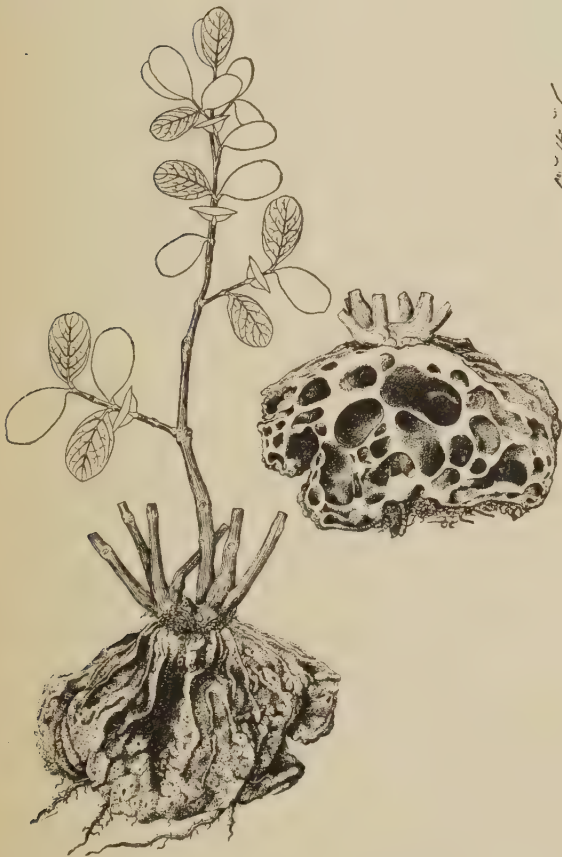


FIG. 176. *Hydrophytum*, an epiphytic plant  
The swollen base of the stem is composed largely of water-storing tissue and contains cavities inhabited by ants. ( $\times \frac{1}{3}$ )



FIG. 177. *Polypodium sinatum*, a fern having hollow, fleshy stems inhabited by ants. ( $\times \frac{1}{3}$ )

storage are underground ones, there are exceptions. Some palms have greatly thickened stems in which large quantities of starch are stored during a series of years. This food is finally used up in the formation of flowers and fruits, after which the stem dies. Commercial sago is made from the starch stored in the trunks of the sago palm.

Some stems are especially thickened and modified for the storage of water. This is particularly true of the cacti (Figs. 512, 514).



FIG. 178. Branches of lime (*Citrus aurantium*) modified as spines. ( $\times \frac{1}{3}$ )

In the Malayan region there are certain curious epiphytic plants that may be mentioned in this connection. The basal portion of the stem is greatly enlarged and consists mostly of water-storing tissue (Figs. 176, 177). In this basal portion are conspicuous labyrinthine cavities which

are connected with the external atmosphere by means of small openings. The cavities are inhabited by ants. Various functions have been assigned to these cavities by different botanists, while others think that they have no particular function. Some regard them as devices for aëration, others consider that the ants which inhabit them benefit the plant by leaving débris from which the plant absorbs nutrient material, while still other observers believe that the ants serve as a means of defense for the plant.

**Protection.** The spines of many plants are modified branches (Fig. 178). In some cases these spines protect the plants to some extent from being eaten by browsing animals.



## CHAPTER VI

### THE ROOT

In general the roots of a plant serve to absorb water and mineral matter from the soil and to anchor the plant in the ground. These may be said to be the chief functions of roots.

**Absorption of water.** The stems, leaves, and fruits of plants are usually exposed to high rates of evaporation in the air, from which they are protected by a covering which is more or less impervious to water. This coating not only reduces the amount of water that they lose through transpiration but at the same time prevents them from absorbing water from the atmosphere. Such plants are therefore dependent on their roots for the absorption of water.

**Absorption of minerals.** Plants not only need water, carbon dioxide, and oxygen, but also nitrogen, sulphur, phosphorus, potassium, calcium, magnesium, and iron. These last elements are obtained from the soil in the form of compounds dissolved in water. Some plants probably require, in addition, sodium and chlorine.

**Anchorage.** Plants that are growing in the ground need roots not only for the absorption of water and mineral matter but also in order that they may be anchored to the substratum; otherwise, erect plants would be blown over by the wind, while small creeping plants might be carried to unfavorable situations. There are three different types of root systems. Many dicotyledonous plants develop a long main root which grows deep in the soil and produces smaller secondary roots; such long roots are called *taproots*. In other cases the plant, instead of having a taproot, is anchored in the ground by several large secondary roots. Monocotyledonous roots, like monocotyledonous stems, do not have secondary thickening, and

so such roots never become very large. Monocotyledonous plants are usually anchored in the ground by numerous small roots. This is conspicuously the case with large palms such as the coconut.

**Aërial roots.** Roots are characteristically subterranean structures, but they may develop in the air. Such is the case with many

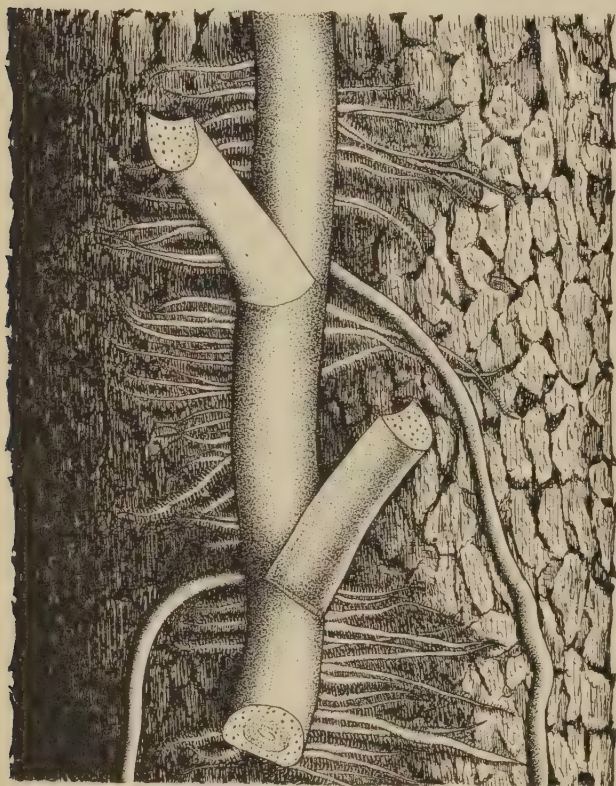


FIG. 179. Climbing stem of *Raphidophora*, showing short roots that attach the stem to the support, and long ones that grow to the ground and absorb water. ( $\times \frac{1}{2}$ )

climbing plants (Fig. 179) and also with epiphytes, which are plants that grow perched on other plants (Fig. 2). In both of these cases the roots still have the functions of absorbing water and anchoring the plant. In epiphytic plants many of the roots grow so close to the bark of the plant on which they are found as to become attached to it. They are, at the same time, in a fairly favorable position for the absorption of water. Certain climbing plants develop two types of roots: small, short roots which anchor the plant to its support, and longer ones

which reach down to the ground and serve more particularly for the absorption of water (Fig. 179).

**Incidental functions.** Roots have not only the two principal functions mentioned above but also functions that are incidental to these, as well as other functions, such as respiration, which are common to all plant parts. We shall find later that water absorbed by the roots is taken in very largely by the small young roots. In order that this water may reach the stem it must pass through the larger roots. In the same way



manufactured food which comes down the stem from the leaves can reach the smaller roots only by passing through the larger ones. Thus it will be seen that roots, like stems, have the incidental functions of conducting food and water. The cells in which such conduction is carried on are alike in roots and stems. Roots, like stems, also serve for the storage of food and are sometimes greatly thickened with storage tissue (Fig. 180).

#### GROWTH OF ROOTS

**Rootcap.** Roots are like stems in having at the tip a growing region, called the *growing point*. As the growing point is composed of meristematic cells which are soft and have thin walls, obviously it must be protected in some way; otherwise the meristematic cells would be

destroyed while being pushed through the soil. This protective function is performed by a cap-shaped structure, the rootcap, which covers the growing point (Figs. 181, 183). The rootcap and the tip of the root are joined at the growing point, which consists of a small group of meristematic cells (Fig. 182). The outer part of the growing point produces cells that are added to the rootcap, while the inner portion forms cells which increase the length of the root.

The rootcap not only protects the growing point of the root but also serves as a boring point. It is especially fitted for



FIG. 180. Radish with greatly thickened storage root. ( $\times \frac{1}{4}$ )

this function because it is conical in shape, and probably even more so on account of the fact that the cell walls, or at least the middle lamellæ of the old cells, become gelatinous. This makes the surface of the rootcap rather slimy, so that friction with the soil particles is greatly reduced and the tip can move through the soil more readily. As the rootcap is pushed forward



FIG. 181. Tip of aerial root of *Pandanus tectorius*, showing rootcap

Compare Fig. 196. ( $\times \frac{1}{2}$ )

through the soil particles the older cells are rubbed off and are replaced by younger ones which are produced from the meristem at the junction of the rootcap and the tip of the root.

**Grand period of growth.** A portion of a root, like any other part of a plant, has a grand period of growth which can be divided into a phase of formation, a phase of elongation, and a phase of maturation. As has been said before, the cells that add to the length of the root are produced on the basal side of the growing point. After these cells are cut off from the growing point they undergo a limited number of divisions. The part of the root in which division is most active is in the phase of formation, and the region in which this division occurs may be termed the region of formation. After dividing a number of times the cells derived from the growing point cease to divide, and elongate very considerably (Fig. 183). The region in which this is taking place most actively is called the region of elongation, and the portion of the root that is elongating is in the phase of elongation. The greatest increase in length of any portion of a root occurs while it is in this phase. Fig. 13 gives an idea of the elongation of an individual cell. After a portion of a root has reached its mature length the cells in that part take on their final characteristics. A region in which this is occurring is in the phase of maturation.



In the case of the root, as in that of the stem, the portion that is in the phase of formation grows slowly. At the end of the phase of formation the rate of growth increases, and

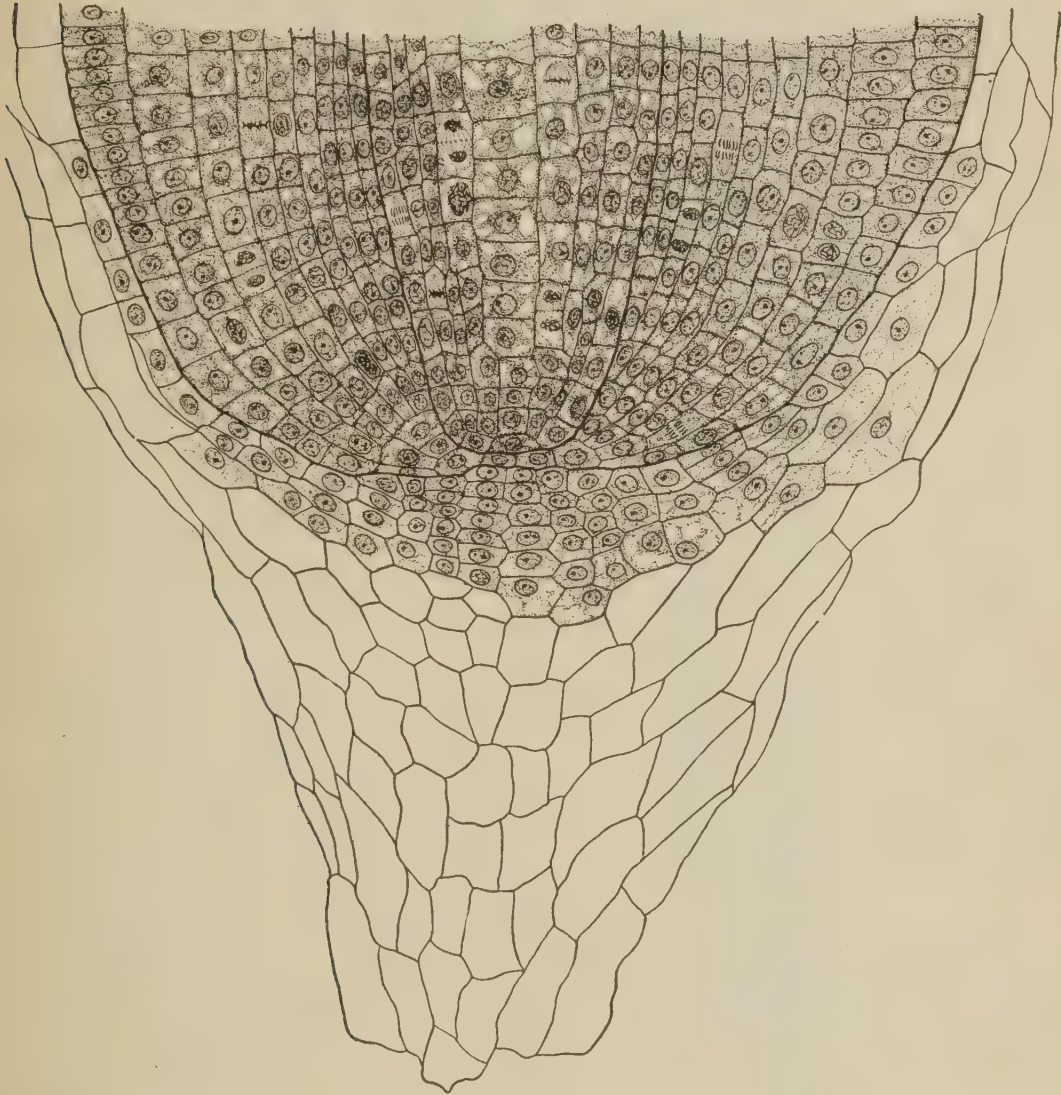


FIG. 182. Longitudinal section of a tip of an onion root

The growing point is in the center of the drawing and consists of three regions: one which produces the rootcap, one which gives rise to the cortex and epidermis, and one which forms the stele. ( $\times 270$ )

continues to increase until the most rapid rate is reached during the phase of elongation. After this the rate of growth in length again decreases until, at the end of the period of maturation, growth ceases altogether. Growth is therefore most rapid not at the tip but slightly back of the tip in the region of elongation.

In general the region of elongation is much longer in stems than in roots. This is probably connected, in part at least, with the fact that the air offers very little resistance to the growth of

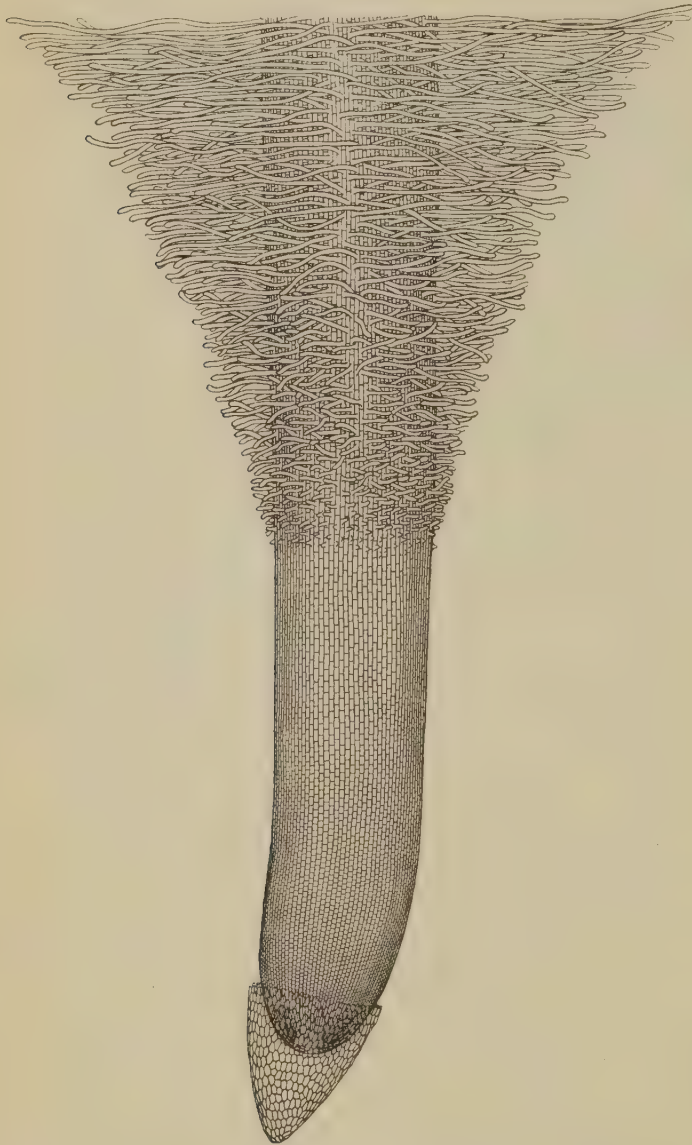


FIG. 183. Tip of root of millet

Below is the rootcap. Above the cap is the region of elongation, and above this a portion of the root-hair zone showing growth of root hairs. ( $\times 35$ )

Enlargement of the surface is produced by the growth of long, slender projections from the cells of the outermost layer, or epidermis, of the root. These projections are called root hairs (Fig. 183). Root hairs are not cut off from the epidermal cells but are simply projections from them (Fig. 184). Most of

stems, while the roots, in growing through the soil, meet with considerable resistance. If the elongating region of a root, which is composed of soft tissue, were of considerable length, the resistance offered to its movement through the soil would cause it to crumple.

#### ABSORPTION OF MATERIALS

**Root hairs.** We have seen that one of the principal functions of ordinary roots is to absorb water. It is therefore essential that they should have a large surface for the performance of this function, as the larger the absorbing surface the greater the rate of ab-



the water absorbed by the roots is taken in by these hairs. They contain a lining of protoplasm within which is a large vacuole. As a root hair is the most active part of an epidermal cell, the nucleus is usually found in the root hair.

Since root hairs serve largely for the absorption of water, it is not surprising to find that many of the plants that grow submerged in water do not possess them.

#### Physical characteristics of the soil.

In order to understand how roots absorb substances from the soil it will be necessary to consider the physical characteristics of the soil itself. The soil is made up of small, irregularly shaped particles of rock and decomposing organic matter, with spaces between the particles. If the soil is well drained these spaces are largely filled with air. The water occurs as very thin films which adhere to the soil particles. The force by which this water is held is very great; it is so great that the water cannot

all be removed by evaporation without the application of heat.

The air found between the soil particles is essential to the respiration of the roots of most plants. The presence of air can be very clearly demonstrated by putting a mass of soil under water, when the water will displace the air in the spaces and the air will be seen leaving the top of the soil in the form of bubbles. Many plants cannot live in a soil that is flooded, as such a soil does not contain sufficient oxygen for the respiration of their roots.

**Contact of root hairs with soil particles.** The formation of root hairs aids in the absorption of water not only because it increases the absorbing surface but also because the hairs come in closer contact with the soil particles than would be possible in the case of large roots.

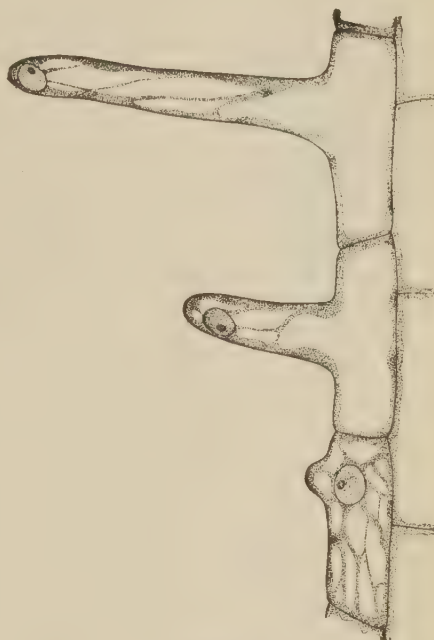


FIG. 184. Section showing the formation of root hairs in millet root. ( $\times 280$ )

**Growth of root hairs.** Root hairs tend to grow out at right angles from the surface of the roots, but when they are in the soil they soon meet with soil particles and are thus turned aside.



FIG. 185. Seedling of radish, showing root hairs grown in moist air. ( $\times 1\frac{1}{3}$ )

In doing this their surfaces conform to those of the particles around which they grow, so that they are in very intimate contact with the soil particles. Growth in root hairs occurs only at the tip, which is protected by having a thickened wall (Fig. 184). Growth at any point other than the tip would loosen the attachment of the hairs to the soil particles.

**Location of root hairs.** Root hairs do not occur at the tip of the root or in the region of elongation. If they did occur in these places, they would, on account of their close contact with the soil particles, be likely to be broken as the tip was pushed through the soil. Root hairs are ephemeral structures, and after they have functioned for a short time they dry up and disappear, so that they occur in only a

short zone, which is called the *root-hair zone*.

**Anchorage by root hairs.** The close contact of the root hairs with the soil particles is of advantage in more ways than simply for absorbing water and minerals from the soil. The contact with the soil particles is so close that when the root is pulled from the soil either the hairs are broken off or the soil particles adhere to the roots (Figs. 185, 186). This adhesion of the hairs to the soil particles aids in anchoring the plant in the ground. It is also of advantage in that the part of the root which bears the root hairs is firmly anchored, so that when the more apical portion increases in length the root-hair zone is held firmly in position and the tip is shoved forward.

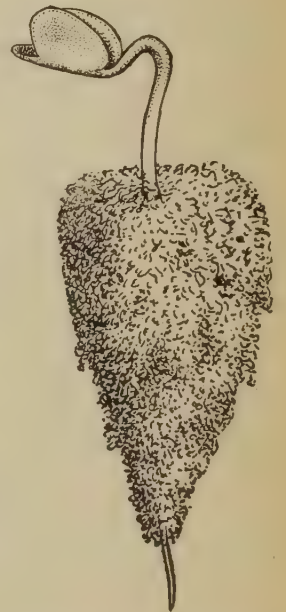


FIG. 186. Seedling of radish from seed planted in the soil. Note the adherence of soil to root hairs and compare with Fig. 185. ( $\times 1\frac{1}{3}$ )



**Absorption of water.** The cell wall of the root hair is lined with a thin layer of protoplasm, within which is a large vacuole that has sugar and other substances dissolved in it. The protoplasm acts as a semipermeable membrane around the vacuole, while the plasma membrane which bounds the cytoplasm is a semipermeable membrane around the remainder of the protoplasm. The osmotic pressure in the root hair is greater than that of the surrounding soil water, and so water is drawn from the soil into the root hair. Osmotic pressure is also instrumental in causing the movement of water from cell to cell in the cortex of the root.

**Passage of water through the cortex.** When water passes into a root hair, it goes from a solution with a low osmotic pressure to one with a high osmotic pressure; when it passes from the parenchyma cells to the vessels, the reverse is the case; but the water is frequently forced into the vessels under considerable pressure. This is clearly shown in the bleeding, or exudation of water, from the stems of many plants after the upper part of the plant has been removed. The bleeding seems to be due to great turgidity and high turgor pressure in the parenchyma cells. When pressure within the cells becomes sufficiently great, water and other substances to which the protoplasm is permeable appear to be forced out of the cells under pressure; but this process is not fully understood.

**Turgor pressure.** The pressure of bleeding is often designated as root pressure because when plants are turgid the roots usually produce such a pressure. *Turgor pressure* is a more appropriate name, however, as pressure of a similar nature may be produced in other parts of plants.

Turgor pressure of roots cannot be considered as an explanation of the movement of water up the stem, as such pressure can occur only when the parenchyma cells of the root are turgid, and this is not usually the case when transpiration is active and the movement of water most rapid. At such times there is little or no turgor pressure, and water may be absorbed by the stump of a decapitated stem instead of being exuded from it.

Bleeding is largely responsible for the exudation of maple sap or the sweet juices from palm inflorescences (Figs. 137, 138) that have been cut and that yield sugar or, after fermentation, produce alcoholic beverages or vinegar. The Mexican alcoholic beverage known as pulque has a similar origin, as it is the fermented juice obtained from agave plants from which the buds have been removed.

**Absorption of minerals.** The water around the soil particles contains mineral matter which is dissolved from the soil. This water is in contact with that in the cell wall of the root hair, and so is continuous with it, while the water in the cell wall is in turn continuous with that in the interior of the hair. The mineral matter dissolved in the soil water tends to diffuse into the water in the cell wall, and through that into the interior of the cell. In this way mineral matter passes from the soil into the plant. While in the root hairs the plasma membrane, or outer layer of protoplasm, is impermeable to sugar and many other substances within the cell, it is permeable to many of the simple inorganic compounds found in the soil. The diffusion of the mineral matter through the plasma membrane is independent of the movement of the water.

By the use of a piece of parchment paper separating a solution of sugar from pure water it is very easy to demonstrate that the movement of a solvent and the movement of the solute through a membrane may be independent of each other. The volume of the sugar solution will increase, showing that it has absorbed water, while at the same time some of the sugar will pass in the opposite direction into the pure water. The movement of water in one direction and of a dissolved substance in the opposite direction, through the same membrane at the same time, can be strikingly shown by the use of the thistle-tube apparatus shown in Fig. 32. The bulb of the thistle tube is filled with concentrated sugar solution, a piece of parchment paper tied over the mouth of the bulb, the tube inverted, and the bulb immersed in distilled water. Water is drawn into the sugar solution, as is shown by the fact that the latter rises in the thistle tube. If



now we repeat the same experiment with the addition of coloring the sugar solution with eosin, the sugar solution still rises in the tube while some of the eosin passes out through the parchment paper and colors the distilled water. In other words, the movements of the eosin and the water are independent.

**Accumulation of mineral matter in a plant.** As movement by diffusion is always from a greater to a less concentration, a given kind of mineral matter would be expected to enter a plant only so long as the concentration of that particular substance was greater outside than inside the plant. The original substance, however, after entering a plant, is usually combined with others in such a way that it no longer exists in the same form as in the soil water. In this way the concentration of a given substance may remain greater outside than inside, even though it is absorbed in large quantities. Owing to this fact a plant may accumulate a much greater proportion of a given element than is found in the soil water.

As the diffusion of mineral matter dissolved in water is independent of the diffusion of the water itself, an increase in the amount of water absorbed by a plant would not increase the amount of mineral matter absorbed if the water moved in the plant only by diffusion. It is only owing to the fact that the water in the vessels moves as a steady stream, and not by diffusion, that transpiration can increase the amount of mineral matter taken in by a plant.

It is indeed questionable how far transpiration can cause an accumulation of mineral matter in a plant. If any given mineral substance should accumulate anywhere in the plant in greater concentration than it occurs in the soil, it would tend to diffuse to a region of lower concentration and finally to the soil water. It is only as a given mineral substance is changed into some other substance that the elements composing it can accumulate in the plant to a much greater extent than that in which they occur in the soil water.

## SOIL

**Texture of soil.** Soils are composed of particles which are classified according to their size as *gravel*, *sand*, *silt*, and *clay*. These divisions are arbitrary, and the size limits assigned to the various classes by different authorities are not always the same. Particles over 1 millimeter in diameter may be regarded as gravel or rock ; those between 0.05 millimeter and 1 millimeter, as sand ; those between 0.005 millimeter and 0.05 millimeter, as silt ; and those less than 0.005 millimeter, as clay. A soil containing a large proportion of sand is called a sandy soil, one with much clay a clay soil, while soils that are intermediate are *loams*.

The amount of water held by a soil varies with the total surface of the particles, and so clay, being more finely divided than sand, holds more water than sand, which dries out rather quickly.

**Movement of water in soil.** During a rain, water enters the spaces in the soil and expels the air. The action of gravity tends to carry the water down into the soil, but films are left around the soil particles. The downward movement of the water is known as *percolation*. After the rain has ceased, air is drawn into the soil as the water moves downward. Percolation continues until a region (the *water table*) is reached in which all the spaces are occupied by water. The percolation of water is most rapid in coarse soils and slowest in fine soils. In clay soil, percolation may be so slow that after the upper layers have become saturated much water runs off the surface, while the underlying layers remain relatively dry.

The percolation of water is very important, as by this means a reserve supply is carried to lower levels. The soil loses water by evaporation from the surface, with the result that water is drawn up from the lower levels in much the same way as oil moves up a wick. Also, when a plant absorbs water from the soil particles in contact with the root hairs, water is drawn from more moist particles to those from which the plant has taken water. It is owing to this movement of soil water that a soil dries out rather uniformly.



Water is drawn up in loam more rapidly than in sand or clay. The attraction of a soil for water increases with the total surface of the particles; consequently loam draws water with greater force than does sand. According to this reasoning we should expect clay to draw water more rapidly than loam; but clay is composed of such small particles, and the spaces between the particles are so small, that water is held with great force and there is less tendency for the water to percolate or be drawn up than in the case of loam.

Loam allows sufficient water to percolate through it, and then draws it up again with considerable rapidity. For this reason loam is better for agricultural purposes than is either sandy soil or clay. Moreover, the air spaces are large enough to allow for sufficient aëration, which is not likely to be the case with clay.

The upward movement of water takes place in the films around the particles, and so any interference with the continuity of the films tends to retard the movement. Water can be conserved by working the soil near the surface into a mulch, or loose layer, as by this means the continuity of the films is interrupted, so that water is not drawn to the surface, where it would be lost by evaporation. That water is drawn to the surface to a greater extent in compact than in loose soil is shown in the case of footprints in a cultivated field. The soil under the footprints is more compact than the surrounding soil and has a darker color due to the greater amount of water that it contains.

**Soil structure.** The term *soil structure* is used to denote the manner in which the particles are arranged in a soil. When the fine particles are aggregated in granules, the soil is said to have a granular, or crumb, structure. Such a soil is loose and friable and is considered to be in good physical condition. If a clay soil is worked when it is wet, the granular structure is destroyed and the soil becomes compact and poorly aërated. The soil is then in poor physical condition. The wet condition is very persistent, and at the same time the soil is impervious to the

percolation of any water. As the clay soil in this wet condition dries it shrinks and cracks, thus forming hard, tenacious clods.

**Weight of soil.** A given volume of sand is heavier than the same volume of clay, as the weight of the individual grains of sand is sufficient to overcome considerable friction and to cause the particles to be compactly arranged, so that the pore space is decreased to a greater extent than is the case with lighter particles such as clay.

Water has a tendency to bind soil particles together, as is shown in the case of sand, which can be molded to some extent when wet but falls apart when dry. Owing to the greater amount of surface afforded by the small particles of clay, water binds particles of clay together with much more force than it does grains of sand. It is partly for this reason that clay is tenacious and harder to plow than sand, and it is owing to these properties that a farmer regards clay as a heavy soil and sand as a light soil.

**Water absorption and transpiration.** When soil contains a considerable quantity of water, it gives up water to plants more readily than when it is dry. The amount of water in the soil may therefore be a very important factor in determining whether or not a given rate of transpiration is excessive. In order that a plant may live it must, over an extensive period, absorb as much water as it loses through transpiration. If the rate of transpiration continues to be greater than the rate of absorption, the plant will ultimately wither and die. When there is a sufficient supply of water in the soil, a plant may be able to replace the amount of water lost, even when the rate of transpiration is comparatively high; while if there is less water in the soil, the same rate of transpiration may cause the plant to succumb to drought.

**Available soil moisture.** Plants not only cannot absorb water as rapidly from a dry soil as from a moist soil, but they will wilt long before all the water is removed from the soil. When the water is reduced below a certain amount, a plant cannot absorb it fast enough to replace loss through transpiration, and



so wilting ensues. Therefore not all the water that is in the soil is available. The percentage of water that is left in a soil when a plant wilts is called the *wilting coefficient* of that soil. This wilting coefficient varies with different soils, being higher with fine soil than with coarse soils. It also varies with the rate of evaporation, as a plant will wilt with more water in a soil when the rate of transpiration is high than when it is low.

**Effects of cultivation.** Cultivation destroys weeds and renders the soil more porous, so that it is better aërated, water is absorbed readily, and roots can penetrate it easily. As previously pointed out, cultivation of the surface layers may decrease the amount of water lost from the soil through evaporation.

**Humus.** Soils contain varying quantities of dark-colored decaying organic matter known as humus. It is owing to the presence of humus in soil that the soil is usually darker colored than the subsoil. As a source of nitrogen, humus is a very important constituent of soils. It is also valuable in other ways. Humus has great capacity for absorbing water and so may have great value in increasing the water-holding capacity of a soil. Clay soil is rendered more porous by the presence of humus.

**Organisms in the soil.** The decay of the organic matter in the soil is due to the action of living organisms, chiefly bacteria and fungi, including the vegetative parts of such forms as mushrooms.

Bacteria are very important in changing organic nitrogen into a form that can be absorbed and used by green plants. By bacterial action ammonia is produced from organic compounds of nitrogen, and the ammonia is then converted into nitrates.

An important class of bacteria is that which has the property of absorbing free nitrogen and uniting it with other elements to form compounds. Such bacteria add nitrogen to the soil and are of great advantage in the maintenance of soil fertility.

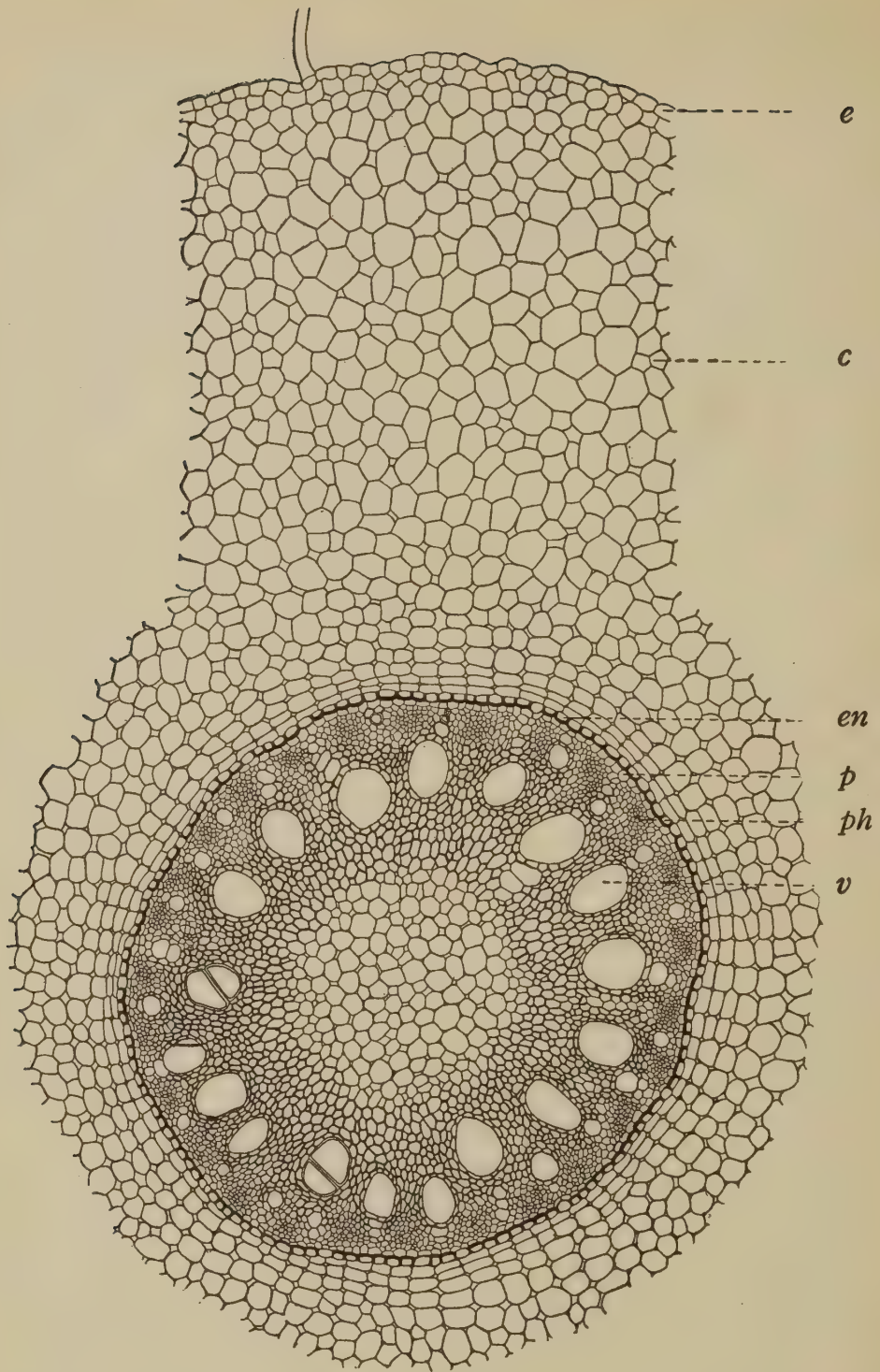


FIG. 187. Portion of section of root of a monocotyledonous plant (*Hedychium coronarium*), showing stele and portion of cortex and epidermis  
*e*, epidermis; *c*, cortex; *en*, endodermis; *p*, pericycle; *ph*, phloëm; *v*, xylem vessel. ( $\times 85$ )



## THE ANATOMY OF ROOTS

**General regions.** The general internal structure of stems and roots is very similar. In both cases there is a central stele which is surrounded by a cortex (Figs. 187, 188). In stems

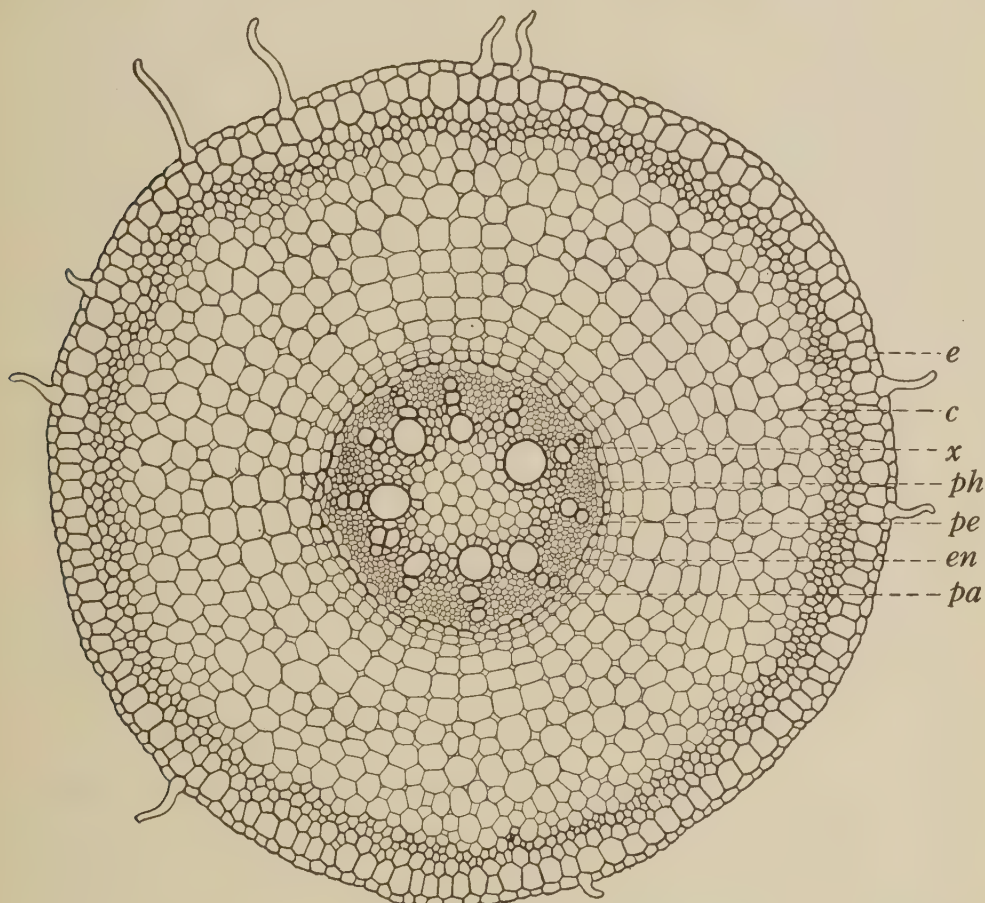


FIG. 188. Cross section of root of a species of Wandering Jew (*Commelina*), a monocotyledonous plant

*e*, epidermis; *c*, cortex; *en*, endodermis; *pa*, passage cell; *pe*, pericycle; *ph*, phloëm; *x*, xylem. ( $\times 55$ )

this is in turn surrounded by an epidermis. Some authorities maintain that in roots there is no true epidermis, but that this structure is represented morphologically in the formation of the primary rootcap. Others, however, contend that the outermost layer of the root is morphologically an epidermis, but that it is not such physiologically, as it is an absorbing and not a protective structure. These theoretical considerations need not

concern us here; for the sake of simplicity we may regard the outermost layer of the root as an epidermis.

**Epidermis.** The epidermis of a root is, as we have seen, very different in structure and function from that of stems and leaves, but agrees with that of the latter in being a single layer of cells.

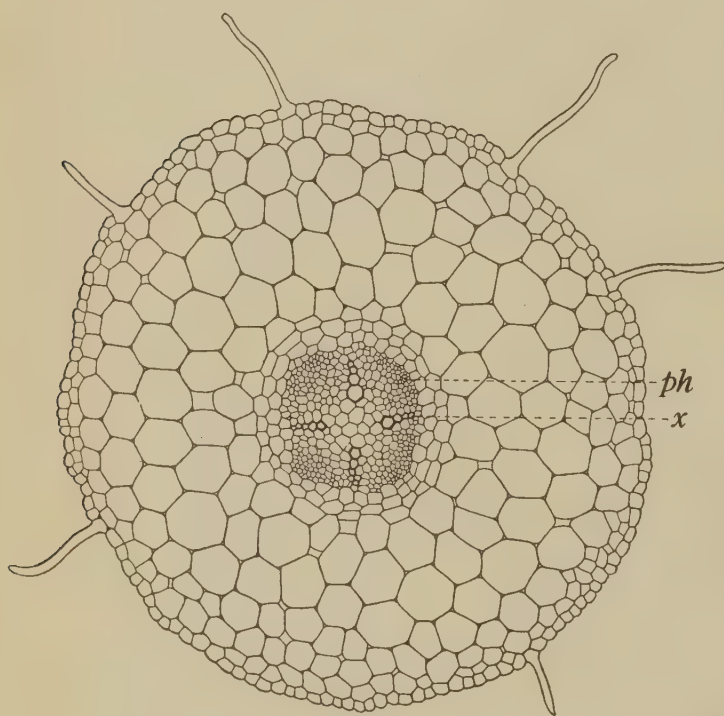


FIG. 189. Cross section of young root of a dicotyledonous plant, mungo bean (*Phaseolus radiatus*)

In the stele there are four rows of xylem vessels, the protoxylem, one of which is labeled *x*. Alternating with the xylem is the phloem, *ph*. ( $\times 70$ )

Roots that grow underground are not exposed to high rates of evaporation, and so they do not need to have cutinized walls to protect them from transpiration. Moreover, if their walls were cutinized or thickened, this would interfere with the absorption of water. The walls are thin, soft, cellulose membranes. The principal peculiarity of these cells consists in the presence of the long root hairs,

the structure and function of which have already been discussed.

**Stele.** The general structure of monocotyledonous and dicotyledonous roots is very similar (Figs. 188, 189). This applies to the arrangement of vascular bundles as well as to other features, and is strikingly in contrast with the great difference in arrangement of bundles in monocotyledonous and dicotyledonous stems.

The stele of roots is usually much smaller in comparison with the cortex than is the case with stems (Figs. 188, 189). This is due to the greater centralization of the thick-walled elements in roots than in stems, which is connected with the fact,



as previously explained, that the stress which roots have to withstand is largely longitudinal tension.

The center of the stele may be occupied by thin-walled pith cells, by thick-walled sclerenchymatous cells, or by one or more xylem vessels. Around this central portion the xylem, as seen in cross section, is arranged in rays which are usually widest near the center and taper toward the outside (Figs. 188, 189). The phloëm occurs in groups between the xylem regions, and not exterior to the xylem, as in stems. The alternate arrangement of the xylem and phloëm is apparently connected with the absorbing function of roots. As the phloëm is not at the outside of the xylem, water may pass straight from the epidermis to the xylem without going through the phloëm.

**Pericycle.** The outermost part of the stele is, as in stems, the pericycle. In roots the pericycle never contains sclerenchyma cells but is composed altogether of parenchyma cells and usually consists of only a single layer (Figs. 188, 192).

**Cortex.** The cortex lies between the stele and the epidermis. The innermost layer of the cortex in the stem is known as the starch sheath. In roots this layer is called the *endodermis*. The walls of the endodermis, particularly the radial ones, are partially cutinized. The walls may remain thin (Fig. 192) or they may be thickened (Figs. 187, 188). In the latter case all the

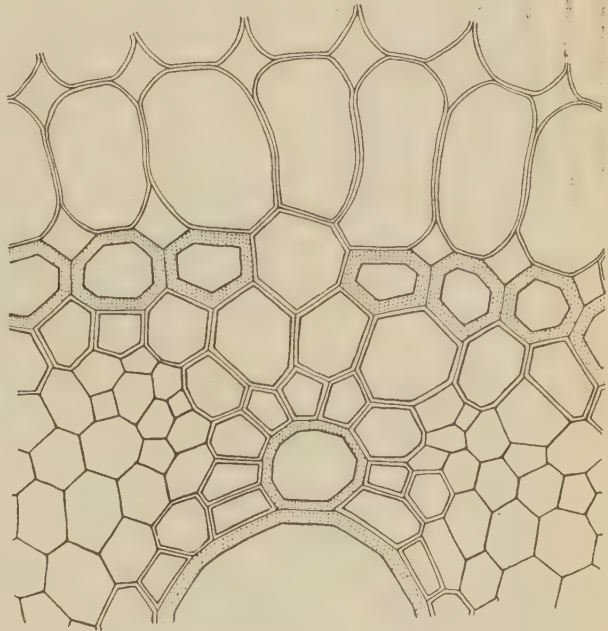


FIG. 190. Cross section of a portion of root of Wandering Jew (*Commelina*), showing endodermis and passage cell

The endodermis is a row of thick-walled cells running across the drawing; the passage cell is the thin-walled cell in this row. Note the xylem below the passage cell. ( $\times 300$ )

walls may be equally thickened, but usually the radial and inner walls are thicker than the outer walls. Certain cells found in the endodermis near the ends of the xylem rays (Figs. 188, 190)

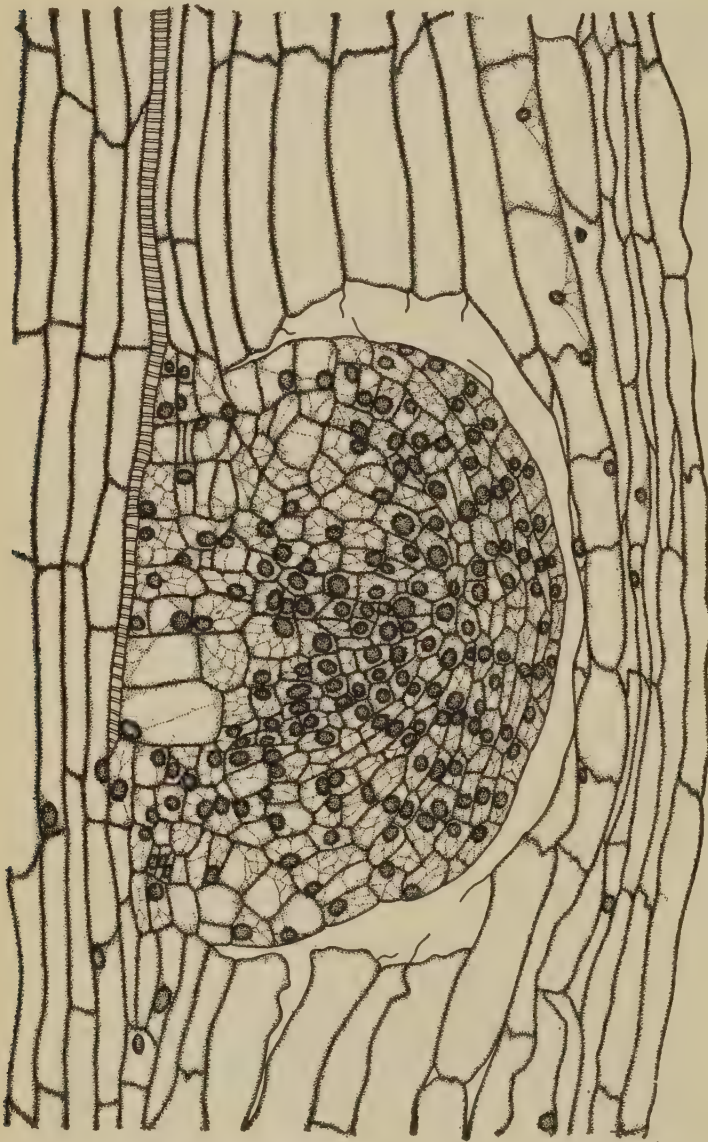


FIG. 191. Longitudinal section of a portion of an onion root, showing internal origin of branch root. ( $\times 175$ )

remain thin-walled as long as that part of the root is absorbing water through its root hairs. Such thin-walled cells are called *passage cells* and apparently serve as passageways for water going from the cortex into the stele. An endodermis containing thin-walled cells and passage cells would appear to serve as a means of directing the movement of water so that as it enters the stele it will pass directly to the xylem and not through the phloëm. The water thus enters the xylem and is conducted upward without getting into the sieve tubes and diluting their contents. In old parts of roots the cortex frequently disappears and the endodermis functions as an epidermis (Fig. 194).

The endodermal cells fit close together, so that there are no air spaces between them. As there are air spaces between the other cells of the cortex, the lack of them in the endodermis would appear to decrease the diffusion of air into the vascular tissues.

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The part of the cortex outside of the endodermis is frequently composed of parenchyma cells only. These cells may serve for the slow movement and storage of food. As in the case of stems the cortex in young roots is of importance in giving rigidity.

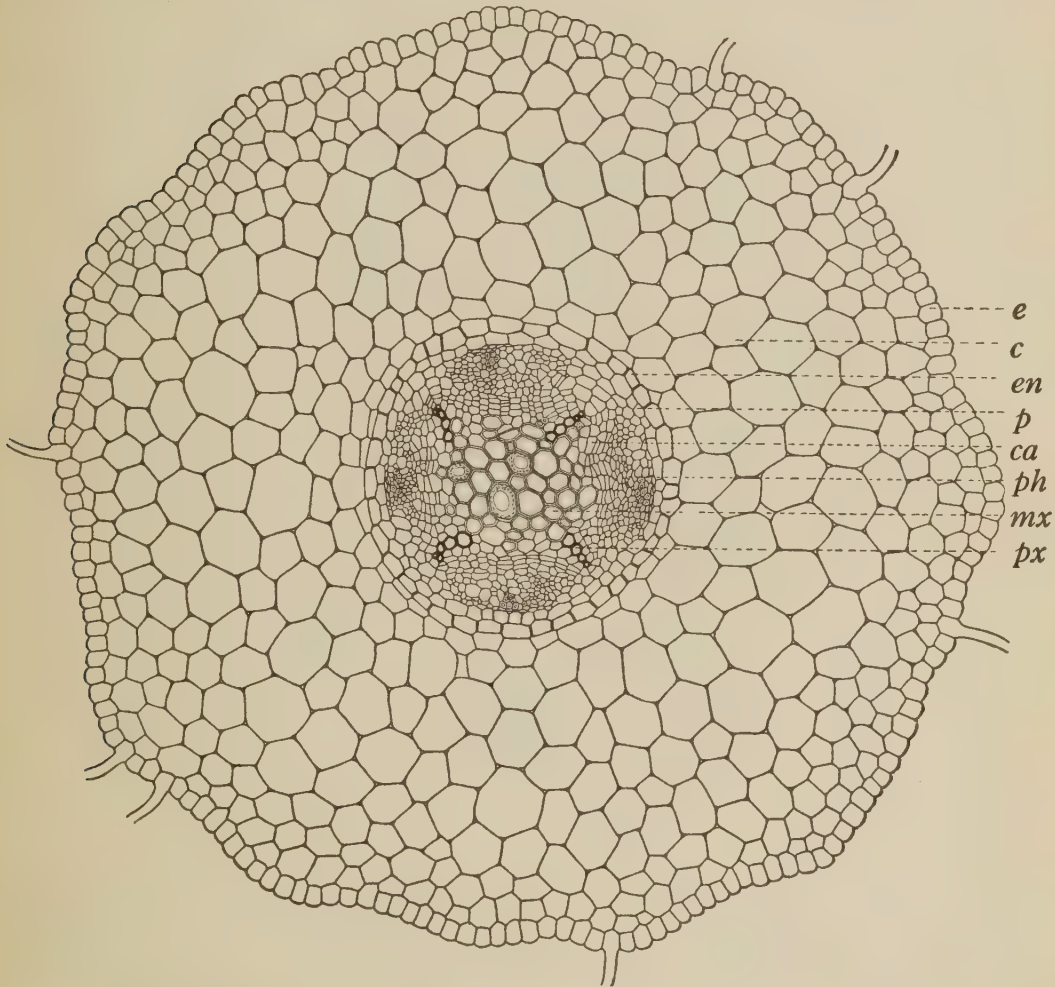


FIG. 192. Cross section of root of mungo bean (*Phaseolus radiatus*) older than that shown in Fig. 189

*e*, epidermis; *c*, cortex; *en*, endodermis; *p*, pericycle; *ca*, cambium region; *ph*, phloem; *px*, protoxylem; *mx*, metaxylem. ( $\times 85$ )

This is done by means of turgor. The epidermis of the root is usually an ephemeral structure. In many cases the cell walls of the outer layers of the cortex become thickened, and these layers take the place of the epidermis.

The cortex of the root does not contain collenchyma, as does that of many stems. In stems the collenchyma usually forms a

continuous band in the outer part of the cortex. As previously explained, this distribution of collenchyma is connected with the resistance which stems have to offer to bending stresses. As roots are not subject to the same type of stresses, there is not the same necessity for the development of collenchyma.

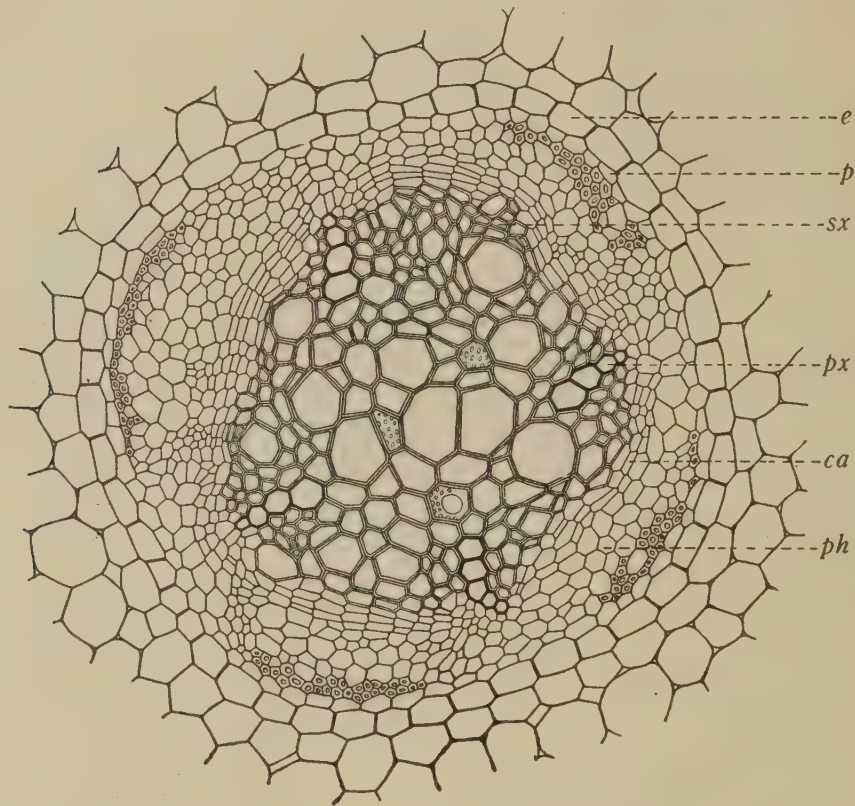


FIG. 193. Cross section of central portion of root of mungo bean (*Phaseolus radiatus*) after secondary xylem has been formed from the cambium  
*e*, endodermis; *p*, pericycle; *ph*, phloëm; *ca*, cambium; *px*, primary xylem; *sx*, secondary xylem. ( $\times 115$ )

Roots that are in the ground cannot carry on photosynthesis, and in such cases chlorophyll is not developed in the cortex. In roots which normally are exposed to the light, however, chlorophyll is frequently developed in the parenchyma cells of the cortex, and in this case the cells are chlorenchyma cells.

**Branch roots.** The branches of stems originate as superficial outgrowths in which both the epidermis and the underlying tissues take part. The cortex and epidermis of the branch and those of the main stem are therefore continuous. In roots, on



the other hand, a branch originates in the pericycle and forces its way through the cortex and epidermis, breaking these tissues as it grows (Fig. 191). Owing to their method of origin,

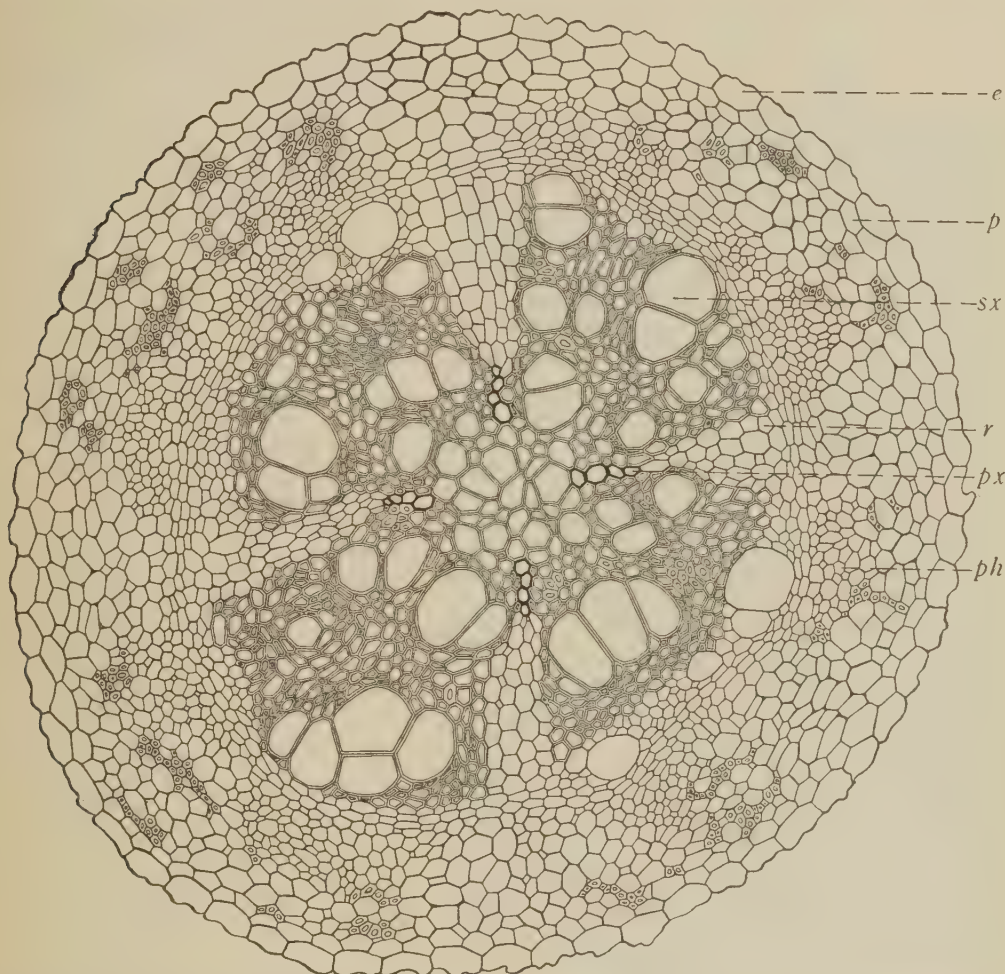


FIG. 194. Cross section of root of mungo bean (*Phaseolus radiatus*) after all of the cortex except the endodermis has disappeared

*e*, endodermis; *p*, pericycle; *ph*, phloem; *px*, primary xylem; *sx*, secondary xylem; *r*, pith ray. ( $\times 80$ )

therefore, the epidermis and the cortex of a branch root are not continuous with the epidermis and the cortex of the main root.

**Secondary thickening.** Dicotyledonous roots, like dicotyledonous stems, increase in thickness owing to the activity of the cambium. In very young roots there is no cambium (Fig. 189). The beginning of the process of secondary thickening is initiated by the formation of a cambium in the stele on the inner side of each group of phloem (Fig. 192). Subsequently this cambium

extends around the outer end of the rays of the xylem, so that it forms a convoluted cylinder (Fig. 192). By the activity of the cambium, secondary phloëm is formed on the inner side of the primary phloëm. The secondary xylem is not formed next to the primary xylem (Fig. 193) but opposite the secondary

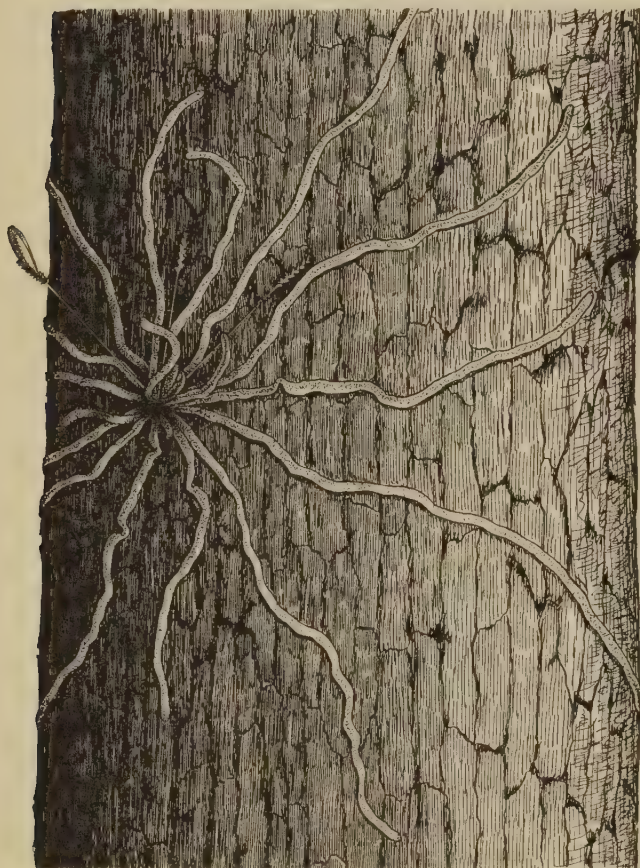


FIG. 195. *Taeniophyllum*, an epiphytic, leafless orchid with roots which serve for photosynthesis. ( $\times \frac{2}{3}$ )

of water and mineral matter and the anchorage of the plant. Some parasites have specialized roots that produce haustoria (Fig. 8) which perform these functions. Moreover, roots, like other organs, may be specialized for functions which are not, in general, characteristic of the organ concerned. Such specialized roots may be classified according to their functions under the following headings: *photosynthesis* (leaf function), *support* (stem function), *reproduction* (seed function), *storage*, and *aëration*.

phloëm, while a pith ray is formed exterior to each of the primary rays of xylem (Figs. 193, 194). Although at first the cambium has the form of a convoluted cylinder, the convolutions are soon straightened out by unequal rates of growth in different places, and the cambium, as seen in the cross section, becomes a regular circle (Fig. 194). The subsequent activity of the cambium of the root is similar to that of the stem.

#### SPECIALIZED ROOTS

The chief functions of roots are the absorption



**Photosynthesis (leaf function).** Underground roots are not exposed to the light, and so are not in a position to carry on photosynthesis. Such roots do not develop chlorophyll. The roots of many epiphytes and of some vines, however, are exposed to the light, and such roots usually possess chlorophyll and so manufacture food by means of photosynthesis. In the epiphytic orchid *Taeniophyllum* (Fig. 195) this function is performed almost entirely by the roots. This plant has no leaves and only a small stem, to which the roots are attached and which bears the flower shoots. The roots, on the other hand, are highly developed and contain chlorophyll.

**Support (stem function).**

In a number of cases, roots take the place of stems in serving as supports. This is the case in the genus *Pandanus* (Fig. 196), where that part of the stem which

is near the ground is very small and incapable of supporting the weight of the plant. Large roots grow out from the main stem and serve to brace it; such roots are called *brace roots*. Other roots grow down from the branches and prop them up; such roots are known as *prop roots*. *Rhizophora* (Figs. 197, 516) has similar brace and prop roots. Corn has brace roots.



FIG. 196. *Pandanus tectorius* with prop roots. ( $\times \frac{1}{35}$ )





FIG. 197. Prop root of *Rhizophora candelaria*

These roots have a great development of air spaces in which oxygen diffuses to the underground portions of the root system



FIG. 198. India rubber tree (*Ficus elastica*) with roots forming secondary trunks



These roots grow out in whorls from the lower nodes and serve to brace the stem of the plant.

Prop roots are conspicuous in many species of the genus *Ficus* (Fig. 198), and particularly in the banyan tree. In the latter case large roots extend down from the larger branches and serve as secondary trunks. As a result one plant may extend over a considerable area and be supported by a large number of prop roots which, from the standpoint of function, may be regarded as additional trunks.

Another very interesting example of supporting roots is afforded by the *strangling figs* of tropical forests. These plants start as epiphytes in the tops of the trees and send down roots that reach the ground (Fig. 199). Branches from these roots grow around the tree and coalesce, either with each other or with the main

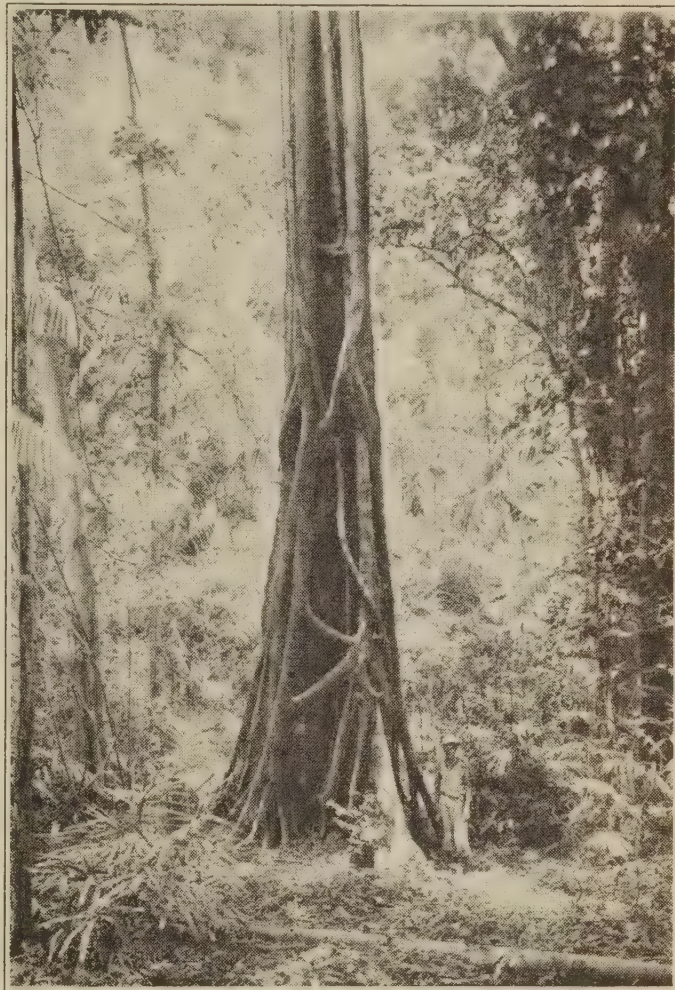


FIG. 199. Roots of strangling fig on a large tree trunk

root, until the trunk of the tree is usually inclosed by a network. As this grows and coalesces, it interferes with the growth of the tree, the fig leaves shade the tree, and the roots of the fig interfere with those of the tree. This combination usually results in the death of the tree on which the fig is growing. The mesh-like support of the fig continues to grow until it may finally have the appearance of a solid trunk. Usually, however, some



of the meshes persist. The final appearance of these figs is greatly influenced by the form and height of the trees on which



FIG. 200. An old specimen of strangling fig in which the roots serve as trunks

they start. When they grow on slanting or peculiarly shaped trees, they sometimes assume very fantastic shapes (Fig. 200).

Climbing plants may be attached to their supports by means of roots and so be supported by the roots (Fig. 179).



Many tropical trees have *buttress roots* (Fig. 492) which are formed by the outgrowth of planklike extensions from the upper portions of large roots. Such buttress roots are frequently made into table tops.

**Reproduction (seed function).** The roots of many plants produce adventitious buds which grow into new plants and thus serve to reproduce the species. Some plants are reproduced artificially by root cuttings.

**Storage.** Underground roots may become very much thickened and serve as organs for the storage of food. Such is the case in sweet potatoes (Fig. 201), yams, radishes (Fig. 180), turnips, parsnips, and carrots. Roots may also store water.

**Aëration.** Specialized aërating roots are found on a number of plants that grow in submerged soil (Fig. 518). These are particularly prominent in mangrove swamps. Such roots contain a conspicuous development of air space. Oxygen from the atmosphere diffuses into these spaces and then down into the underground root system. The aërating roots extend vertically out of the soil in some mangrove-swamp species (Fig. 517), and also in the bald cypress of the fresh-water swamps of the southeastern part of the United States. In the genus *Rhizophora* (Fig. 197) of the mangrove swamps the aërating roots grow from the trunk and branches and also serve as absorbing roots and as brace and prop roots.



FIG. 201. Root of sweet potato modified for food storage. ( $\times \frac{1}{4}$ )

## CHAPTER VII

### THE FLOWER

The flowers of plants are reproductive structures whose function is the production of seed. Many flowers are very beautiful, are greatly enjoyed by man, and are used by him for purposes of ornament. From the standpoint of the plant, however, the beauty of the flower is important only in so far as it aids in the production of seed.

#### REPRODUCTION

**Asexual reproduction.** Plants have two methods of reproduction, *sexual* and *asexual*. The latter method consists simply in the separation of a portion from the parent plant and the growth of this portion into a complete plant. Many of the lower plants are reproduced asexually by a single cell. A large number of higher plants reproduce vegetatively by sending out shoots which take root and produce new plants (Fig. 5). In many cases the part of the shoot which connects the two plants dies, thus leaving them entirely separate. This method is particularly characteristic of plants with underground or prostrate stems, such as grasses that have long runners. It is also frequently seen in the aërial parts of plants, where a shoot takes root and produces a new individual. Another method of asexual reproduction is the production of bulblets. Many plants that grow from underground bulbs reproduce by the multiplication of these bulbs, as is the case with the onion. Bulbs may be produced on flowering shoots as in *Agave* and the onion. Many plants produce suckers which can be removed and used to produce new plants. Conspicuous examples are bananas (Fig. 66) and pineapples. A method of artificial reproduction frequently



used is to cut off a portion of a stem, known as a cutting, and plant it in the ground. Under favorable conditions the cutting produces roots and leaves and grows into a new plant. In a few instances leaves of plants may fall to the ground and grow into new plants, as in *Bryophyllum* (Fig. 83) and *Begonia*. A considerable number of plants can be artificially reproduced by the use of leaf cuttings. Some ferns reproduce regularly by having the tip of a long leaf reach the ground, send out roots, and grow into a new plant (Fig. 82).

**Sexual reproduction.** Sexual reproduction is reproduction in which two cells unite to form a single one from which a daughter organism develops. This method of reproduction is characteristic of the vast majority of plants. Among the higher plants the flower is the organ for sexual reproduction.

#### THE STRUCTURE OF THE FLOWER

**Parts of the flower.** In a complete flower, that is, one which has all the parts of a typical flower, there are four kinds of structures besides the stalk (Figs. 202, 203). There are one or more *pistils*, *stamens*, a *calyx*, and a *corolla*. The pistils and stamens are the essential parts, while the others are accessory.

Some flowers are *regular*, — that is, all the members of each set of organs are alike (Figs. 202, 210–213), — while others are *irregular* (Fig. 204).

**Pistils.** The pistils are usually found in the center of the flower (Fig. 203). A pistil consists of an enlarged basal portion called the *ovary*; a terminal part known as the *stigma*; and, usually, a long, slender structure, the *style*, which connects the ovary with the stigma. The ovary contains one or more cavities (Fig. 205) within which are found small oval or egg-shaped *ovules*. An ovule is attached to the ovary wall by a small stalk



FIG. 202. Flower of *Muntingia calabura*. ( $\times 1\frac{1}{2}$ )

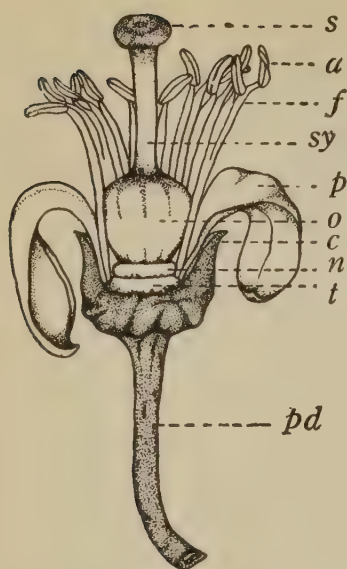


FIG. 203. Flower of grapefruit (*Citrus*) with a portion of calyx and some of petals and stamens removed

*pd*, pedicel; *t*, torus; *n*, nectary; *c*, calyx; *p*, petal; *f*, filament of stamen; *a*, anther; *o*, ovary; *sy*, style; *s*, stigma. ( $\times 1$ )



FIG. 204. Irregular flower of a legume, *Erythrina fusca*. ( $\times \frac{1}{3}$ )

called the *funiculus*. Each ovule contains an *egg* which is the female reproductive cell.

**Stamens.** A stamen consists of two parts (Fig. 206): a large terminal portion, which is the *anther*, and a stalk known as the *filament*. The anther contains cavities called *pollen sacs*, in which *pollen grains* are produced (Figs. 206, 207). Pollen grains from the anthers are carried by the wind, by insects, or by other agencies and deposited on the stigma of the pistil. This transfer is known as *pollination*, and when it has taken place the flower is said to be *pollinated*.

**Fertilization.** A pollen grain, after being deposited on the stigma, produces a long tube which grows down through the stigma and style and enters one of the ovules in the ovary (Fig. 4). Two male nuclei are found at the end of this tube. One of these enters the egg of an ovule and fuses with the nucleus of the egg. This fusion of male and female nuclei is called *fertilization*, and the flower is said to be *fertilized* when this has taken place. After fertilization the ovule develops into a seed, while the whole ovary becomes a fruit.

**Sexuality of flowers.** Usually stamens and pistils are found in the same flower (*bisexual flowers*) (Figs. 202, 203), but frequently they occur in different ones (*unisexual flowers*). When they



occur in different flowers, both kinds of flowers may be on the same plant (*monœcious* plants) (Figs. 208, 209), as in the cases of corn and the castor-oil plant, or they may be on different plants (*diœcious* plants) (Figs. 210, 217).

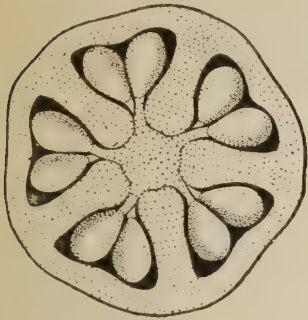


FIG. 205. Cross section of an ovary of *Hibiscus*, showing five cavities or cells containing ovules. ( $\times 10$ )

**Perianth.** While the stamens and pistils are the essential parts of a flower, they are usually surrounded by thin, expanded structures which collectively constitute the *perianth*. In a complete flower the perianth is divided into an interior part, or *corolla*, and an outer part, or *calyx* (Figs. 202, 203).

**Corolla.** The corolla may be composed of a number of separate thin units, the *petals* (Fig. 211), which are white or brightly colored, or of a more or less tubular (Fig. 212), bell-shaped, or funnel-shaped structure (Fig. 213) with lobes which represent the petals. The function of a conspicuous, brightly colored



FIG. 206. Cross section of anther, with pollen grains and pollen sac. ( $\times 85$ )

Below, two types of stamens

corolla seems to be to attract insects or, sometimes, small birds which carry pollen from one flower to another. Brightly colored or conspicuous flowers are usually pollinated by insects.

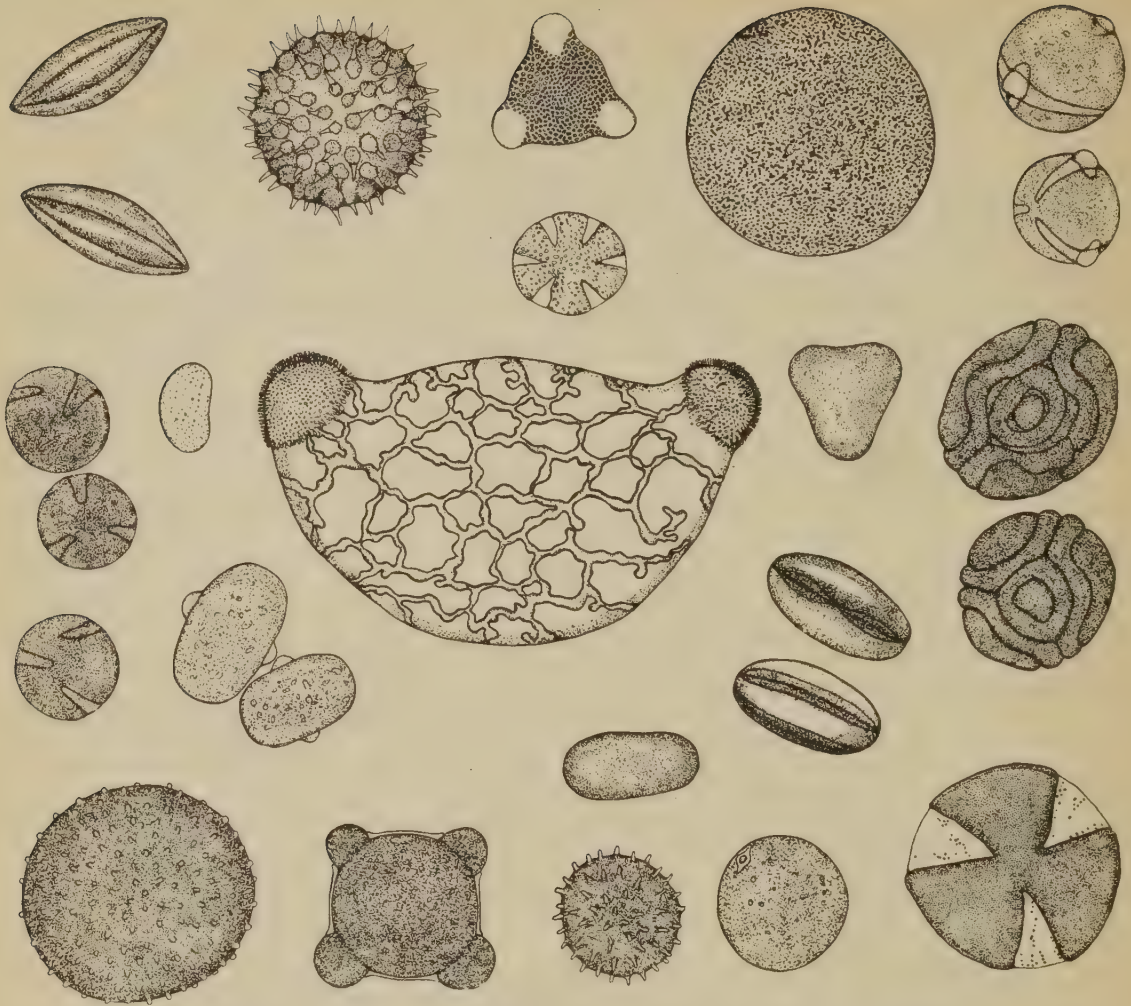


FIG. 207. Pollen grains of various plants. ( $\times 225$ )

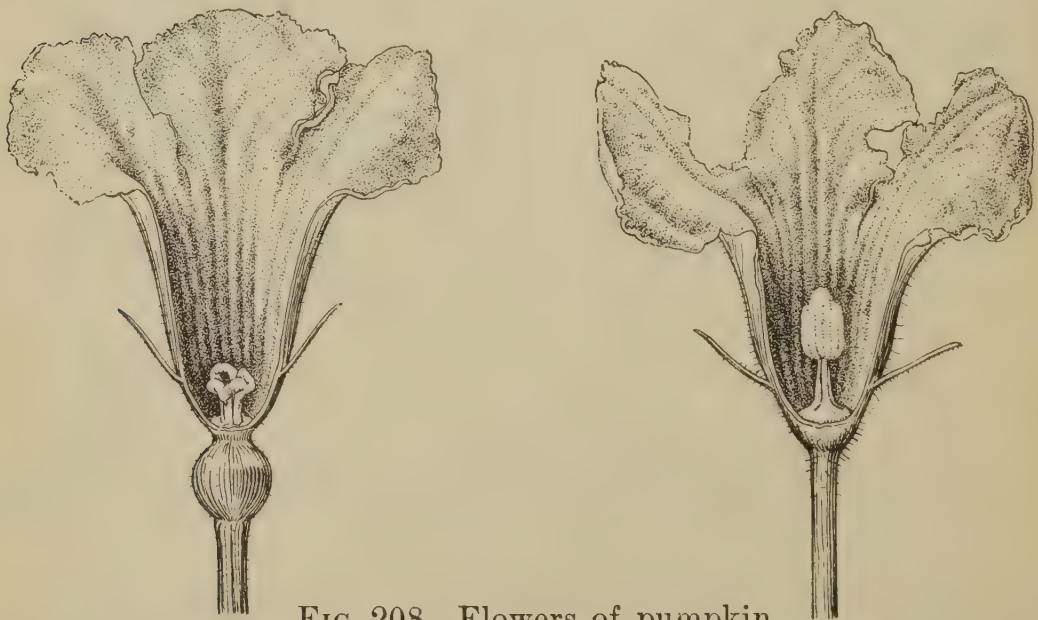


FIG. 208. Flowers of pumpkin

Left, female flower with calyx and corolla attached above rounded ovary ;  
right, male flower. ( $\times \frac{1}{2}$ )





FIG. 209. Flowers of castor-oil plant

Above, female flowers; below, male flowers. ( $\times 1$ )

colored, and very similar in appearance to the petals (Fig. 214).

**Flower stalk.** The flowers are joined to the stem by a central axis, or stalk, which is usually composed of two parts: the stalk proper, which is known as the *pedicel*, and an expanded terminal portion, the *torus*, or receptacle, on which the other parts of the flowers are borne (Fig. 3).

**Calyx.** The calyx, like the corolla, may be composed of a number of separate units, which in this case are called *sepals* (Fig. 202), or of a somewhat tubular or funnel-shaped structure with lobes which represent the sepals. The calyx is typically small and green. The function of the calyx seems to be to protect the inner parts of the flower before the flower bud has opened.

Frequently the perianth consists of only one set of structures, and in such a case this set is regarded as a calyx, the corolla being considered as absent. When there is no corolla, the calyx is often bright-colored and conspicuous and takes the place of the corolla in its function of attracting insects. In many of the monocotyledonous plants the sepals are large, bright-



FIG. 210. Flowers of papaya (*Carica papaya*)

Left, female; right, male. ( $\times \frac{2}{3}$ )



FIG. 211. Flower of *Hibiscus*

The filaments of the stamens are united to form a tube which surrounds the style. ( $\times \frac{2}{3}$ )



FIG. 212. Flower of *Tabernaemontana pandacaqui*

The corolla is composed of a long tube with five prominent lobes. ( $\times \frac{2}{3}$ )



FIG. 213. Flower with a bell-shaped corolla. ( $\times \frac{1}{2}$ )

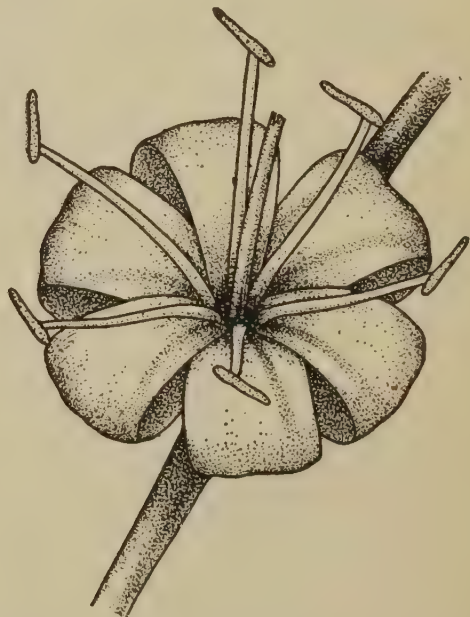


FIG. 214. Flower of *Cordyline terminalis*, showing similarity of petals and sepals



## THE CLASSIFICATION OF PLANTS

In dealing with the very large number of plants that occur in the world it is necessary not only to have names for the various species but also to have a system of classification that groups plants together according to their similarities and relationships. The different kinds of plants are regarded as different species, and each kind is given a species, or specific, name. The structure of the flower is the most important criterion in the classification of flowering plants.

In classifying plants the different kinds (*species*) are grouped into genera, families, orders, classes, and divisions. The whole plant kingdom is divided into *divisions*, one of which, the *Spermatophyta*, includes all seed plants. Divisions are subdivided into *classes*. The classes of the *Spermatophyta* are gymnosperms (seed plants without flowers in the popular sense) and angiosperms (flowering plants). The monocotyledons and dicotyledons are subclasses of the flowering plants. An *order* is a large group which includes plants that have some prominent characteristics in common and show a natural relationship to each other. An order includes one or more related families. A *family* is therefore a subdivision of an order and consists of a group of closely related genera, although a family may contain only a single genus if this genus is distinct enough from all others to be put into a separate family. Usually, however, there are a number of genera in each family. A *genus* is commonly a group of closely related species, but may contain only a single species. A *species* represents a single kind of plant, the individuals of which differ from each other only in minor characters which are bridged over by intermediate forms, and in characters which are due to age, sex, nutrition, individual peculiarity or accidents, or selective breeding by man. The individuals of a species may be cross-pollinated and reproduce the same kind of plant.

The species, genus, family, and order have each a separate name. In writing the name of a plant we use the generic and the specific name. The generic name is written first and then

the specific name. The generic name always begins with a capital letter. According to the most widely accepted usage a specific name is always begun with a small letter. Some botanists, however, prefer to begin the specific name with a capital letter if that name is derived from the name of a person. When the specific name is not derived from a proper noun, it always begins with a small letter. As an example we may take the coconut, which belongs to the genus *Cocos* and has the specific name *nucifera*. We write first the name *Cocos* and begin it with a capital *C*. This is followed by the name *nucifera* (meaning "nut-bearing"), which is begun with a small *n*. The name is therefore written *Cocos nucifera*. As another example we may take the cultivated coleus. This plant belongs to the genus *Coleus* and has the specific name *blumei*. According to the most widely accepted usage this name is written *Coleus blumei*. The name *blumei* was given in honor of the Dutch botanist Blume. Owing to the derivation of the name, some botanists prefer to write it *Blumei*. Specific names frequently refer to some character of the plant, as *nucifera* (nut-bearing), *odorata* (fragrant), *microphylla* (small-leaved), *pinnata* (pinnate-leaved). In other cases the name may be derived from a country, as *americana*; or from the name of a man, as *blumei*; or from one of various other sources. Generic names are similarly derived.

The generic name is regarded as a proper noun and is applied to only one genus in the whole plant kingdom. It is therefore begun with a capital letter. The specific name is regarded as a common noun and may be applied to different species in many genera.

Owing to the fact that the specific name may be applied to a large number of species in different genera, the specific name is never correctly used except in connection with the generic name. The generic name, on the other hand, may be used alone, as it applies to only one genus. As an example we may take the case of the cannas. These plants belong to the genus *Canna*, so that when we use the generic name *Canna* it has a definite meaning, as we know at once that it applies to the cannas. One



of the wild cannas is called *Canna indica*. If we were to use the word *indica* alone, it would not have any definite meaning, as other species in different genera are also named *indica*.

When the name of a plant is written for exact scientific determination, it is customary to place after it the name, or an abbreviation of the name, of the man who gave the specific name to the plant. The name *Cocos nucifera* was given by Linnæus, who is regarded as the father of systematic botany. His name is usually abbreviated L. or Linn. When exactness is required, the name of the coconut should be written *Cocos nucifera* L. or *Cocos nucifera* Linn. The necessity for this arises from the fact that in the development of botanical classification the same name has been applied by different authors to different plants.

The use of scientific names is necessary in order to have names that will be generally understood in all languages, because in different languages the same plant usually has different names. Also, the use of scientific names prevents confusion even in the same language, as in different regions the same common name may be applied to different kinds of plants, or the same plant may be known by different names. A very good example is the word *corn*. It may mean any small, hard seed, as that of the apple, coffee, or any one of the cereals, as wheat or rye. The name *corn* is also used specifically for an important cereal crop of a given region. In England it is applied to wheat; in Scotland and Ireland, to oats; and in the United States, to Indian corn, or maize. It will be seen that one common name may mean different things to different people, whereas the scientific name of Indian corn, which is *Zea mays*, has the same meaning to any botanist, no matter where he may be.

The use of two names has many advantages. The generic name signifies the group to which the plant belongs, and the specific name the individual kind of plant. When the two are used together, we immediately know the individual plant, and we also have an idea as to what are its closest relatives. Another important point is that it would be very difficult to find a sufficient number of names to enable us to give a different

and appropriate one to each species. Genera are much less numerous than species, so it is not so difficult to get enough names for the genera. The use of the same specific name in many genera makes it much easier to find a sufficient

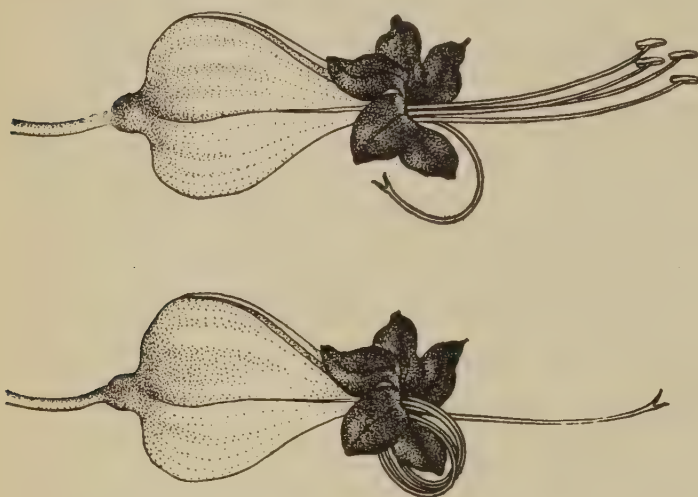


FIG. 215. Flowers of *Clerodendron*

Above, presentation of stamens; below, presentation of stigma, the stamens having coiled under the petals. ( $\times 1$ )

number of appropriate names for the different species.

The earliest books on the classification of plants in which our modern system of names was used were written in the Latin language, and at the present time it is customary to write generic and specific names with Latin endings. For this reason they are regarded as foreign words and so are printed in italics in scientific books and articles. This method has the advantage of making the names more prominent and shows at a glance what plants are discussed in any paragraph.

## POLLINATION

**Cross-pollination.** Most flowers are so arranged as to facilitate the transfer of pollen from the stamens of one flower to the stigma of another (*cross-pollination*) rather than from the stamens to the stigma of the same flower (*self-pollination*). When the stamens and pistils occur in different flowers, the flowers must be cross-pollinated. Cross-pollination is also usual in bisexual flowers. One of the simplest arrangements which assures this is the maturing of the stigmas and anthers at different times (Fig. 215). The most usual agents for the transfer of pollen from one plant to another are insects and wind. Other agencies,



such as small birds, may be effective. In submerged plants the transfer may be made by water.

**Wind-pollination.** Some flowers have no perianth at all, and others very inconspicuous ones. In such cases the pollen is frequently produced in large quantities and is carried by the wind from one flower to another. Indian corn is a good example of a plant that has inconspicuous flowers and is wind-pollinated. The male flowers occur at the top of the plant in what is commonly known as the tassel. The female flowers are produced lower down in heads, which after fertilization become the ears of corn. The long, silky hairs which project from these ears are the styles and stigmas. The female flowers are thus in a favorable position to have pollen blown to them from the male flowers of other plants.

Grasses, many trees, and some shrubs and herbs are wind-pollinated. In order to insure pollination, wind-pollinated species produce large quantities of pollen; and when the pistils and stamens occur in separate flowers, the male flowers are very much more numerous than the female ones. The production of large quantities of pollen is evidently necessary when most of it must be wasted, as is the case with wind-pollinated species, where it is only by rare chance that a grain of pollen will be blown to the stigma of the same species. The stigmas of wind-pollinated plants are usually broad and feathery, and so afford a large surface for catching pollen (Fig. 216). This naturally increases the chance of pollen's reaching the stigma. Many

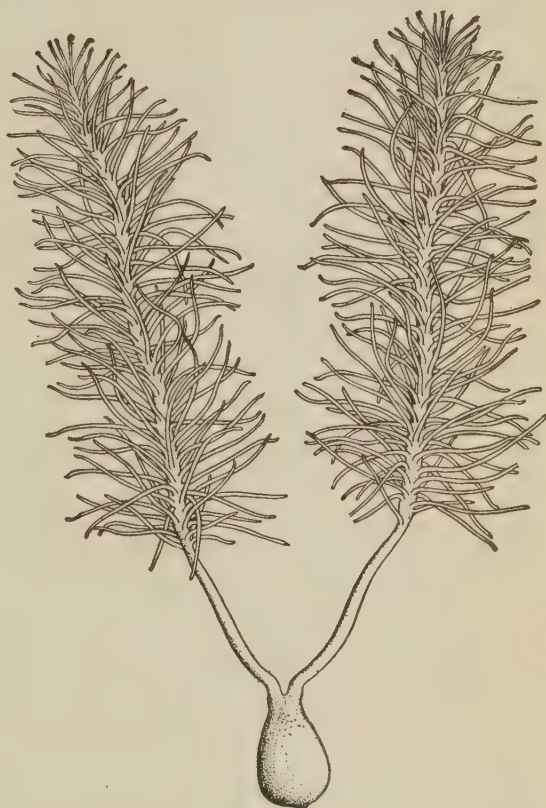


FIG. 216. Feathery stigmas of a grass. ( $\times 12$ )

wind-pollinated species produce their flowers above the foliage, as is usually true of grasses, or at a time when they do not



FIG. 217. Pollination of *Vallisneria gigantea*;  
size of flowers exaggerated

Left, a female plant with a flower floating on the surface of the water; right, a male plant with two spikes of male flowers. The covering of the spike at the left is open and the flowers are becoming detached and rising to the surface, where they open and float. The stamens of one male flower are in contact with the stigma of the female flower

a few species, than in the forests of the moist tropics, where the stand as a rule is made up of a great variety of trees.

have leaves, as is the case with many trees of the temperate zone which produce their flowers early in the spring before the leaves have appeared. Either of these arrangements increases the chance of pollen's reaching the stigma.

Wind-pollination is especially adapted to species which grow together in large numbers, rather than to those which are scattered in mixed stands. Since grasses often cover quite extensive areas, they are very well adapted to this method of pollination, as are also forest trees which grow in stands of one or a few species. Wind-pollination is much more frequent in the forests of the temperate zone, which are composed of one or



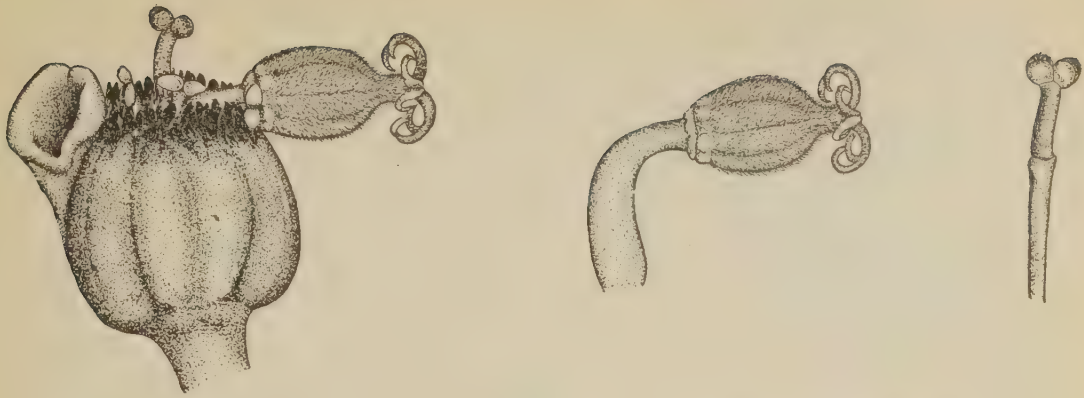


FIG. 218. Flowers of poinsettia (*Euphorbia pulcherrima*)

Left, flower head — at the left of the head is a cup-shaped nectary, and projecting from the head are three male flowers and one female flower; center, a single female flower composed of a stalk and pistil; right, a single male flower composed of a stalk and a single stamen. Compare with Fig. 80. ( $\times 2\frac{1}{2}$ )



FIG. 219. Flower cluster of a legume, rain tree (*Enterolobium saman*), showing brightly colored stamens. ( $\times \frac{1}{3}$ )



FIG. 220. Showy flower head of a legume, *Leucaena glauca*  
The conspicuousness of the head is due to white stamens and pistils. ( $\times 1$ )



FIG. 221. Flower of *Canna*

Below is the ovary surmounted by three small sepals, within which are three narrow petals. The conspicuous parts are the stamens, the central one of which bears an anther on the margin to the left. In the center of the flower is the stigma. ( $\times \frac{2}{5}$ )



FIG. 222. Flower head of bachelor's button (*Gomphrena globosa*)

The flowers are small, and each is surrounded by two conspicuous white or brightly colored specialized leaves or bracts. ( $\times 1$ )

bodies of the pollinating insects are usually hairy. When the stigma of a flower is mature, it has a sticky surface to

**Insect-pollination.** Insects are attracted to flowers by their odor, by their conspicuousness, or by both odor and conspicuousness, and visit them for the purpose of collecting nectar and pollen, which serve them as food. While visiting a flower the body of an insect becomes dusted with pollen, which may subsequently be caught on the stigma of another flower visited.

*Nectar* is a sweet liquid that is secreted by glands which may be on the torus (Fig. 203) or on the petals. Conspicuous cavities in the petals frequently contain nectar glands. Bees use nectar in making honey.

Many flowers that do not secrete nectar produce large quantities of pollen, which serves as food for insects. Although the insects may use a considerable part of the pollen, nevertheless some of it sticks to their bodies and is carried to the stigmas of other flowers.

Insect-pollinated species frequently have pollen which either is sticky or is furnished with numerous projections which help make the pollen adhere to the body of an insect, while the



which pollen grains adhere when the stigma is touched by a part of an insect on which pollen has been caught.

**Water-pollination.** A few species of submerged water plants have female flowers that lie on the surface of the water and male flowers that become detached, float to the female flowers, and deposit pollen on the stigmas. A well-known example is the common eel grass, *Vallisneria* (Fig. 217).

**Conspicuous flowers.** In typical flowers the conspicuous part is the perianth, but in many insect-pollinated species the perianth is lacking or inconspicuous, while other structures are showy and serve for the attraction of insects (Figs. 80, 218).

In *Acacia* and many others of the bean family the perianth is inconspicuous, but a large number of flowers with long stamens are crowded together into a showy, rounded, feathery ball (Figs. 219, 220).

In *Canna* the calyx and corolla are rather inconspicuous, and the bright-colored part of the flower is composed of petal-like stamens (Fig. 221).

In many species the flowers themselves are small and inconspicuous but are surrounded by large, brightly colored, leaflike bracts (Figs. 81, 222). In the family *Ara-ceae* a large number of small flowers are crowded together on a long stalk. The whole flower shoot is more or less surrounded by a large white or bright-colored bract called a spathe (Fig. 223).

In many cases individual flowers are not showy themselves but are crowded together in groups which are very conspicuous. In the family *Compositae* this condition is carried so far that the individual flowers are crowded into heads which superficially

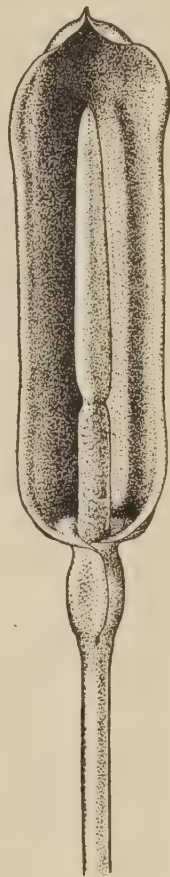


FIG. 223. Flower cluster of elephant's-ear (*Alocasia indica*)

The inflorescence is in the center, the upper part being sterile and the lower bearing numerous flowers; the whole is surrounded by a specialized leaf called a spathe.

( $\times \frac{1}{4}$ )

resemble single flowers (Figs. 224, 225), as is the case with the sunflower, cosmos, daisy, and chrysanthemum.

**Odors of flowers.** Many flowers possess odors which serve to attract insects, and a large number of inconspicuous flowers are pollinated by insects that are attracted by the odor. Conspicuous



FIG. 224. Single flower ( $\times 1\frac{2}{3}$ ) and flower head ( $\times \frac{1}{3}$ ) of a sunflower (*Helianthus cucumerifolius*)

In the single flower the parts from below upward are ovary, calyx, corolla, stamens, and stigma

flowers frequently have odors, although in many cases they are odorless. The odors are due to *essential oils* which are volatile and odoriferous.

The essential oils of flowers are extensively employed in the manufacture of perfumes, toilet waters, and face and sachet powders. Various methods such as steam distillation, extraction with fats (preparation of flower pomades), and extraction with volatile solvents are used to obtain the perfume oils from flowers.

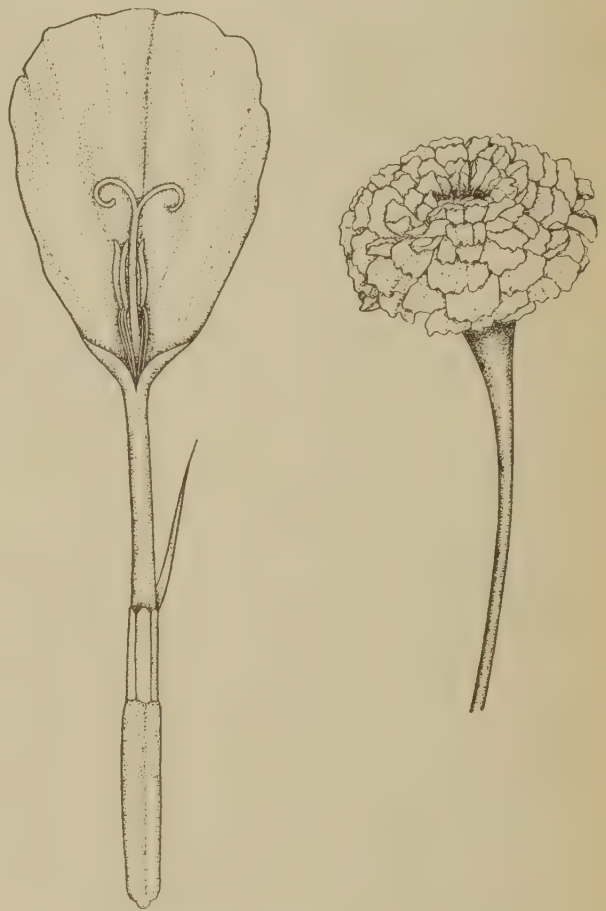


FIG. 225. Single flower ( $\times 2$ ) and flower head ( $\times \frac{1}{2}$ ) of marigold

In the single flower the expanded portion is the corolla; in the center of this are shown the style and the stigma surrounded by stamens



## FERTILIZATION

**Growth of pollen tube.** The transfer of the pollen from the anthers to the stigma is known as pollination and is followed by the growth of the pollen tube which leads to fertilization. After the pollen grain has been deposited on the stigma, it sends out a protuberance, or *pollen tube* (Fig. 226), which grows down through the style till it reaches the ovule. In passing through the style the tube absorbs nourishment from the cells of the style. After reaching the ovary the pollen tube, continuing to grow, enters an ovule (Fig. 4).

There are three nuclei in the pollen tube. One of these is known as the tube nucleus and appears to govern the activity of the pollen tube; the other two are male nuclei. Their functions will be better understood after we have considered the ovule.

**Structure of ovule.** The ovule (Fig. 227) consists of a central mass, the *nucellus*, which is joined to the ovary wall by a

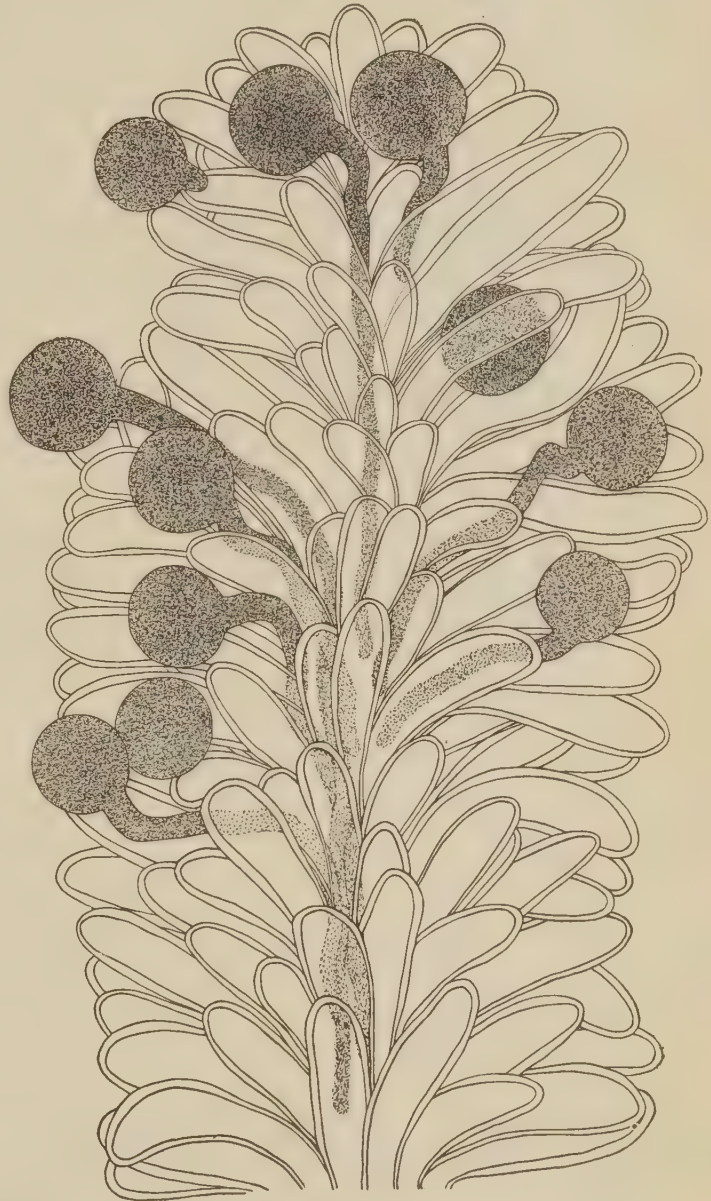


FIG. 226. Germination and growth of pollen grains on a stigma of the purslane (*Portulaca oleracea*). ( $\times 165$ )

stalk, the *funiculus*, and is surrounded by two cellular membranes, the *integuments*. The ovule may be straight, but more usually it is bent back on the funiculus, with the outer integument fused to the funiculus, as shown in Fig. 227. The end of the nucellus that is attached to the funiculus is known

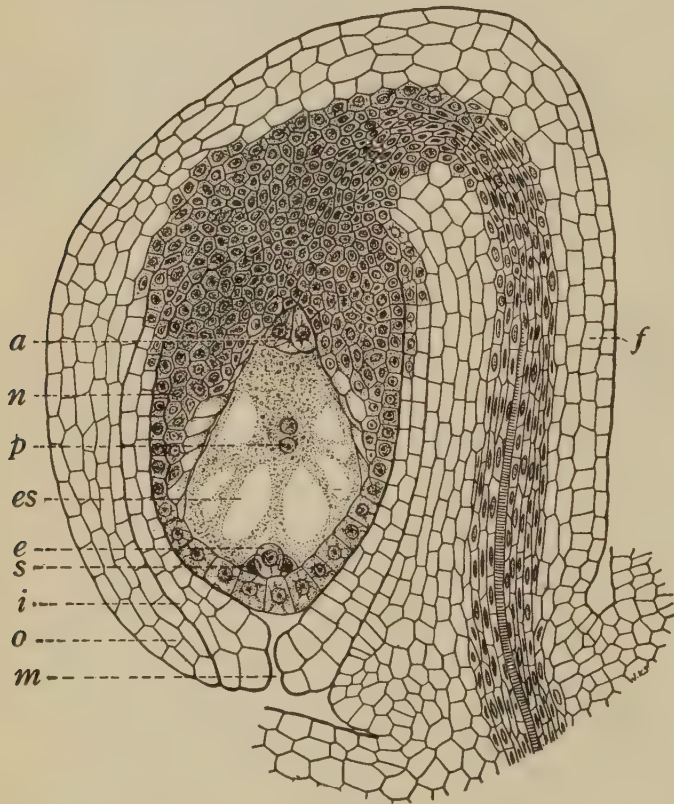


FIG. 227. Ovule of *Zephyranthes rosea*

*f*, funiculus; *m*, micropyle; *o*, outer integument; *i*, inner integument; *n*, nucellus; *es*, embryo sac; *s*, synergid; *e*, egg; *p*, polar nucleus; *a*, antipodal cell. ( $\times 115$ )

as the *chalazal* end. At the opposite end of the ovule there is an opening, the *micropyle*, which extends through the integuments, and through which the pollen tube passes when it enters the ovule. In the nucellus at the micropylar end is the *embryo sac*, which is usually somewhat oval. Within this embryo sac there are six cells and two free nuclei, the *polar nuclei*. The cells occur in a group of three at the micropylar end and another group of three at the chalazal end. The three at the micropylar end consist of a large cell, the *egg*, and two small cells, the *synergids*. At the chalazal end of the sac the three cells are usually small and are known as *antipodals*. The two polar nuclei originate one at each end of the embryo sac, but later move to the center.

**Fertilization.** When the pollen tube reaches the ovule, it grows through the micropyle (Fig. 228) and then into the embryo sac, where it discharges the two male nuclei. One of these enters the egg and fuses with the nucleus of the egg. This



process is known as fertilization, and the product as the fertilized egg. The fertilized egg develops into an embryo, which is found in the seed, and the embryo in turn, after the germination of the seed, grows into a mature plant.

**Endosperm.** The male nucleus which does not fertilize the egg moves to the center of the embryo sac and fuses with the two polar nuclei to form a single nucleus known as the *endosperm nucleus*. This endosperm nucleus rapidly undergoes successive divisions and forms a mass of tissue, the *endosperm*, which fills the embryo sac and surrounds the embryo. The endosperm absorbs nourishment from the surrounding tissue and passes it on to the embryo. The endosperm may be entirely absorbed by the developing embryo before the seed becomes mature, or it may remain in the seed and surround the embryo in the mature seed and be absorbed only during the germination of the seed (Fig. 269).

### THE NUCLEUS

Since the essential part of fertilization consists in the fusion of the male nucleus with the egg (or, more particularly, the male nucleus with the egg nucleus), it is important that the structure of the nucleus should be studied in connection with fertilization.

**Resting nucleus.** The nucleus when not in a state of division is called a resting nucleus. This designation is somewhat unfortunate, as the nucleus of an ordinary cell must be carrying on many activities even though no morphological changes may be evident.

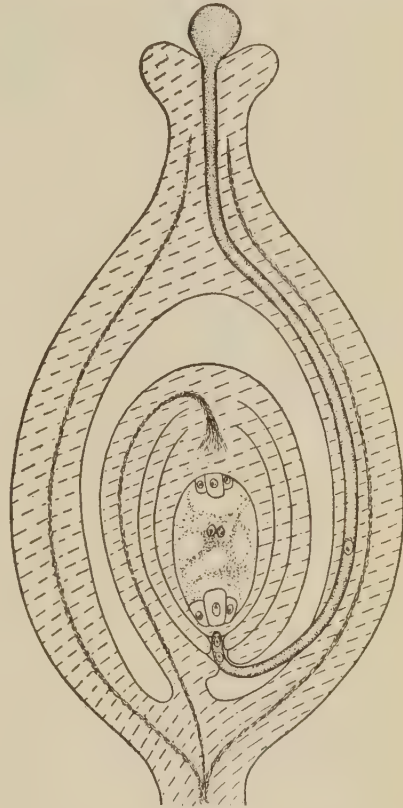


FIG. 228. Diagram of section of ovary, showing growth of pollen tubes toward embryo sac

Within the ovary is a single ovule; in the center of the ovule is the embryo sac surrounded by the nucellus and this by two integuments. A pollen tube has grown from the pollen grain on the stigma and has entered the ovule through the micropyle

The nucleus (Fig. 229, *A*) is usually rounded and is surrounded by a membrane known as the *nuclear membrane*. Within this there is a clear substance, the nuclear sap or *karyolymph*, which is not readily stained. Embedded in the karyolymph is a network, or *reticulum*. This is usually said to be composed of *linin* on which another substance, *chromatin*, is distributed. Chromatin is very easily stained, so that it is conspicuous in stained preparations. The nucleus also usually contains one or more rounded bodies, the *nucleoli*. The function of the nucleoli is somewhat obscure, and it is probable that they have various functions in different cells. In general, however, the nucleolus would seem to be a mass of accumulated material which is usually, though not always, utilized in the metabolic processes of the nucleus.

**Mitosis.** The division of the cell is initiated by the division of the nucleus. In the ordinary method of division a nucleus passes through many stages, and the whole complicated process is known as mitosis. Its chief function seems to be to divide all parts of the chromatin equally between the two daughter nuclei. Mitosis may be considered as consisting of the following stages: *prophase*, *metaphase*, *anaphase*, and *telophase*.

**Prophase.** The initiation of the division of the nucleus is marked by the resolving of the reticulum into a number of more or less distinct units, the *chromosomes* (Fig. 229, *B, C, D, E*). These chromosomes are frequently arranged end to end in a more or less continuous thread (*spireme*), which later segments transversely into separate chromosomes. Sometimes, however, the chromosomes are independent from their first formation. The material of the chromosomes condenses and becomes more or less evenly distributed along the length of the chromosomes. This results in giving them a dense appearance. The chromosomes may be variously shaped, but they are perhaps most frequently somewhat long and slender.

While the chromosomes are being formed, *fibrils* make their appearance in the protoplasm surrounding the nucleus. These fibrils assume such a position that they radiate from two points, called *poles*, on opposite sides of the nucleus. The nuclear



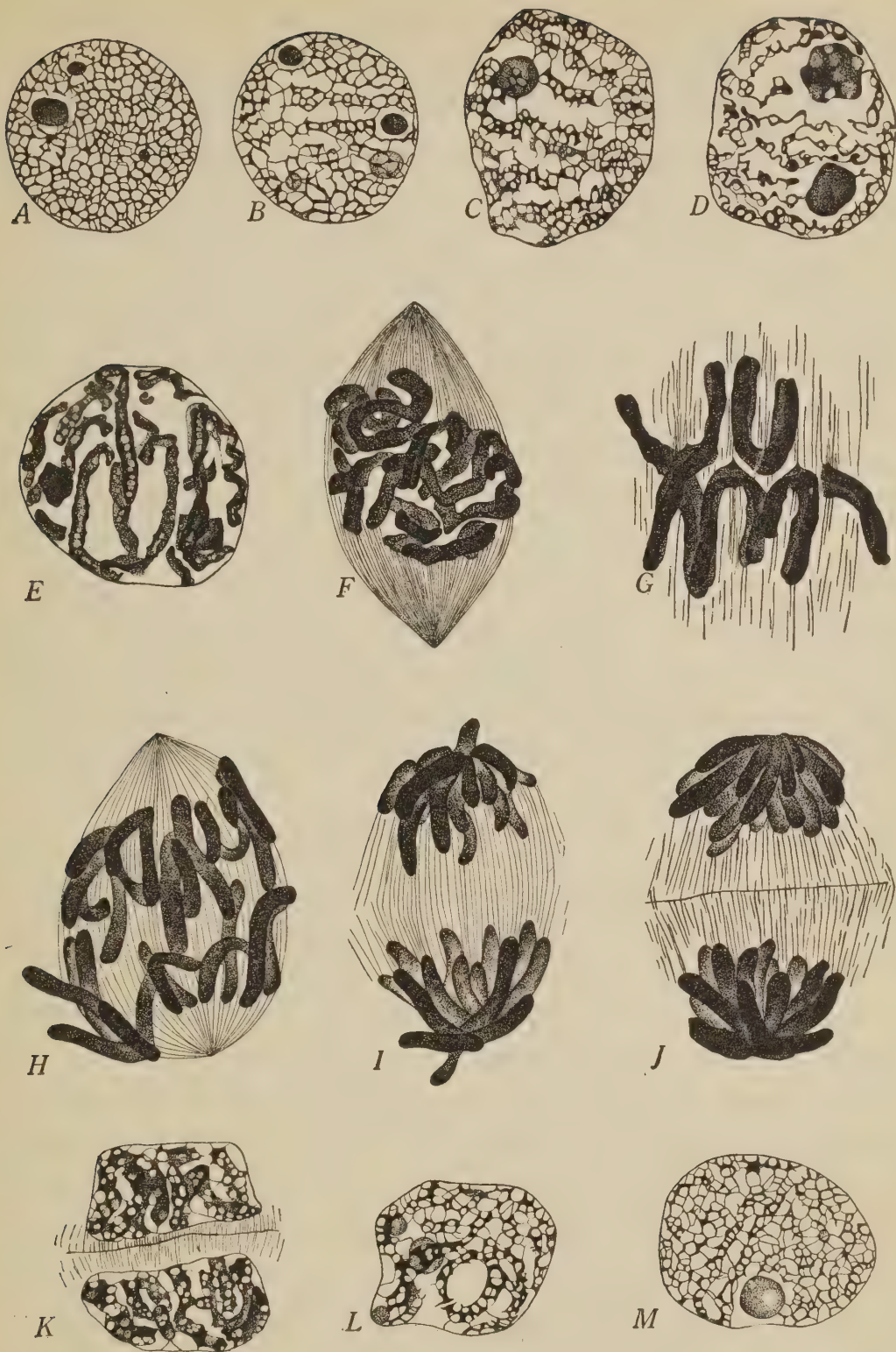


FIG. 229. Successive stages in division and reorganization of nuclei of *Tradescantia*

All except *H* and *I* redrawn after Sharp. ( $\times 1500$ )

membrane disappears, and the fibers grow into the nucleus. Some of them become connected with the chromosomes, while others stretch from pole to pole. At this stage the whole collection of fibers assumes the shape of a spindle, and collectively they are called the *spindle* (Fig. 229, *F*).

After the growth of the spindle fibers into the nucleus and the disappearance of the nuclear membrane the karyolymph becomes mixed with the surrounding cytoplasm. As both nuclear membrane and karyolymph disappear and become mixed with the cytoplasm, and do not form part of the daughter nuclei, they cannot be regarded as permanent cell organs. During the early stages of prophase the nucleolus usually becomes steadily smaller and may disappear altogether, indicating that it constitutes a store of reserve material which is drawn on during the process of division. If the nucleolus persists after the disappearance of the nuclear membrane, it lies free in the cytoplasm and finally disappears. Like the nuclear membrane and nuclear sap it cannot, therefore, be considered as a permanent part of the nucleus.

**Metaphase.** As the fibers form the spindle the chromosomes quickly become arranged in a single plane at the equator of the spindle. The stage during which they are in this position is called metaphase (Fig. 229, *G*). By the end of metaphase each chromosome has separated lengthwise into two daughter chromosomes. The splitting, however, may take place before metaphase and even as soon as early prophase.

**Anaphase.** After metaphase one of each pair of daughter chromosomes travels to one pole, and the other chromosome of each pair to the opposite pole (Fig. 229, *H*). The stage during which the daughter chromosomes move from the equatorial region of the spindle toward the poles is known as anaphase.

**Telophase.** When the chromosomes reach the poles, they collect into a more or less solid-appearing mass. This marks the beginning of telophase (Fig. 229, *I, J*). Soon clear droplets of karyolymph appear within the mass of chromosomes and also between the outermost chromosomes and the cytoplasm (Fig. 229, *K*).



Where the karyolymph comes in contact with the cytoplasm a nuclear membrane is produced. The formation and enlargement of the spaces containing karyolymph continue (Fig. 229, *L*) until the chromosomes again become scattered in the form of a network typical of the resting stage (Fig. 229, *M*). As the mass of chromosomes becomes more and more spread out by the formation of karyolymph a new nucleolus makes its appearance.

**Formation of cell walls.** As the chromosomes become collected at the poles small thickenings are formed on the fibers in the

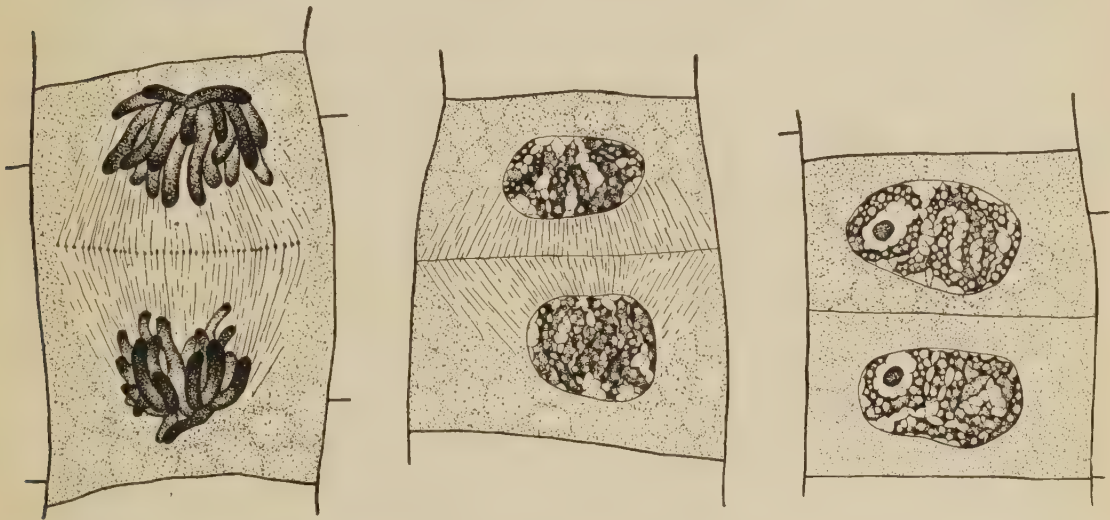


FIG. 230. Successive stages in the formation of a cross wall between two daughter cells in *Tradescantia* root tip. ( $\times 1300$ )

equatorial region. The fibers gradually spread out until the sides of the spindles reach the sides of the cell walls, and the thickenings grow until they form a membrane across the original cell, dividing it into two (Fig. 230). Subsequently new cell walls are deposited on the sides of this membrane, the membrane itself being the site of the middle lamella.

**Individuality of the chromosomes.** The number of chromosomes in a nucleus varies greatly with different species but is constant for the same species. The chromosomes are believed to retain their individuality through the resting stage of the nucleus, and so from one cell generation to the next. In other words, the same chromosomes that pass to a pole in the anaphase of one division reappear during the prophase of the

succeeding division. During the organization of a daughter nucleus from a group of chromosomes the chromosomes become connected by anastomoses. When the chromosomes reappear in the succeeding prophase these anastomoses break down and the chromosomes are separate except in so far as they may be joined together, end to end, in the spireme. Indeed, where cell divisions follow each other in rapid succession the spreading out of the chromatin during the resting stage may not go far enough to obscure the identity of the individual chromosomes.

In following the process of division we have seen that the nuclear membrane, the karyolymph, and the nucleoli disappear during division and are formed anew during the organization of the daughter nuclei. The chromosomes not only appear to persist from one cell generation to the next but they are the only parts of the nucleus that do so. For this and other reasons they are generally regarded as the most important constituents of the nucleus and as the site of the mechanism or factors which determine the hereditary characteristics of an organism.

**Chromosomes and fertilization.** During the process of fertilization the male nucleus and the egg nucleus come together and the sides that meet become flattened against each other. The parts of the two nuclear membranes that are in contact disappear, and thus the contents of the two nuclei come to be inclosed by a single nuclear membrane, a part of which comes from the male nucleus and a part from the egg nucleus. In this way the chromosomes which were in the male nucleus are added to those which were in the egg nucleus. The fertilized egg thus contains the chromosomes of both the egg nucleus and the male nucleus, or, usually, double the number of chromosomes that were in either of the fusing nuclei.

When the fertilized egg nucleus divides, every chromosome splits into two, and one of each pair of the resulting chromosomes goes to each daughter nucleus. In this way each daughter nucleus contains the same number of chromosomes as the nucleus of the fertilized egg. The chromosomes divide in the same manner in the second and all subsequent nuclear divisions in the



vegetative parts of the organism, and so the same number of chromosomes are distributed to every cell in these parts.

**Reduction of the number of chromosomes.** If the same number of chromosomes as are found in the vegetative nuclei went into the egg and sperm nuclei, the fertilized egg of each generation would contain twice as many chromosomes as the nuclei of the preceding generation. This result is prevented by the presence of one division in the life cycle in which the number of chromosomes is reduced to half that found in the ordinary vegetative nuclei. In flowering plants this reduction takes place before the formation of pollen grains, and also before the development of the embryo sac.

Each anther produces a number of cells known as pollen mother cells. By two successive divisions each pollen mother cell gives rise to four pollen grains. The reduction in the number of chromosomes takes place in the first division of the pollen mother cell, so that the nuclei of the pollen grains, and consequently the male nuclei, contain half the number of chromosomes found in ordinary vegetative nuclei.

The formation of the embryo sac is preceded by the development of a single, rather large cell called the megaspore mother cell. This gives rise, by two successive divisions, to four cells which are known as megaspores. The reduction in the number of chromosomes takes place during the first division of the megaspore mother cell. Typically, three of the megaspores degenerate and disappear, while the other develops and produces the embryo sac. The nuclei of the embryo sac, including the nucleus of the egg, thus resemble the male nuclei in containing half the number of chromosomes found in the ordinary vegetative nuclei. The union of the male nucleus with the female nucleus gives the fertilized egg the same number of chromosomes as were in the fertilized egg of the preceding generation. Thus the same number of chromosomes is preserved from generation to generation.

**Heterotypic mitosis.** The division in which the number of chromosomes is reduced is known as the heterotypic division. In the prophase of this division there is a stage which is

not found in ordinary nuclear divisions. During this stage the chromosomes become joined together in pairs.

As a result of this the chromosomes, instead of taking their places on the spindle singly, do so in pairs. In all other

divisions each chromosome splits longitudinally; but during this division, instead of each chromosome's splitting, the members of each pair separate, so that only half as many chromosomes pass to the poles in the anaphase of this division as in the preceding division.

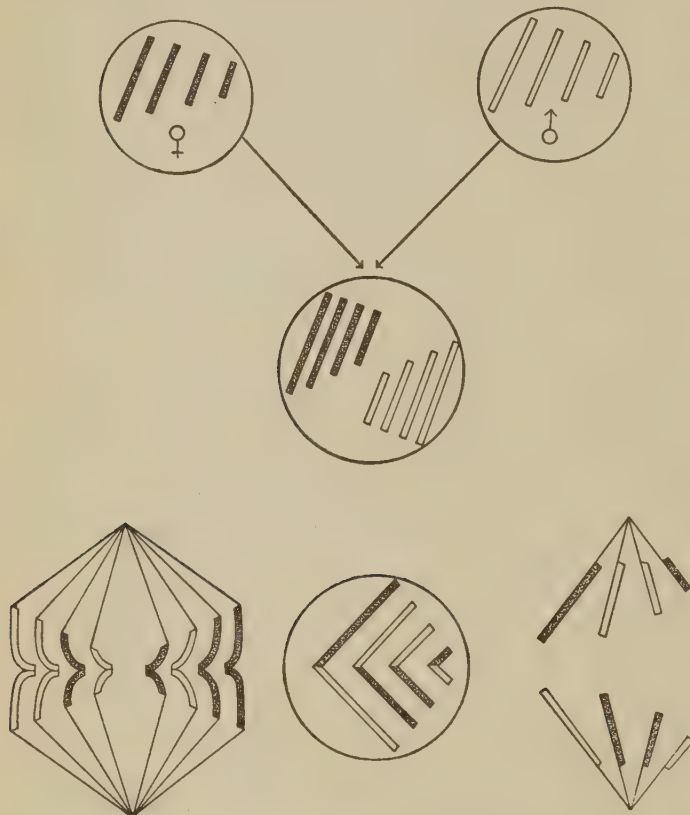


FIG. 231. Diagrammatic representation of the behavior of chromosomes during fertilization and reduction

For convenience in tracing the history of the chromosomes, those from the male nucleus are shaded. Above is the union of male and female nuclei to form the fertilized egg; lower left, division of fertilized egg; lower center, union of chromosomes from the male and egg nuclei in pairs in prophase of reduction division; lower right, the constituents of the pairs of chromosomes have separated at metaphase of reduction division

apparently similar to the complete set in the egg nucleus. The fertilized egg thus has two complete sets of chromosomes.

When two chromosomes unite in the prophase of the heterotypic division, these seem to be not dissimilar but similar

The different chromosomes are believed to carry different hereditary factors, and in some cases the individual chromosomes can be distinguished from each other by differences in size and shape. The chromosomes in the male nucleus appear to differ from each other, while the complete set in the male nucleus is



chromosomes, one of which came from the egg and the other from the sperm nucleus. The result of this union in pairs of similar chromosomes in the prophase, and their later separation, is that each daughter nucleus receives a similar set of chromosomes. In other words, if a daughter nucleus formed by the heterotypic division receives four chromosomes, it is believed that these four chromosomes are all different, and that each is similar to a chromosome found in the sister nucleus. Fertilization and the heterotypic division are shown diagrammatically in Fig. 231.

While a set of chromosomes in the egg nucleus of one plant is believed to carry a set of hereditary factors very similar to the set in any egg or male nucleus of the same species, these sets of factors are not necessarily identical, as different individuals within the same species frequently show different hereditary characteristics.

## CHAPTER VIII

### HEREDITY AND EVOLUTION

#### HEREDITY

The fact that, in general, offspring tend to resemble their parents has been known from early times. The modern conception of the definite laws of heredity, however, is of comparatively recent date and may be said to have begun with Mendel. In 1865, after eight years of investigation, Mendel read the results of his work before the Natural History Society of Brünn, and the following year published them in the transactions of that society. Unfortunately his results were neglected until independent investigations by three botanists led to their rediscovery in 1900. It was then found that Mendel had discovered fundamental laws of heredity. The type of inheritance described by him is now known as *Mendelism*.

#### MENDELISM

**Color inheritance in the four-o'clock.** The subject of inheritance can best be introduced by means of a few examples. If red-flowered four-o'clock plants are crossed with white-flowered ones, the offspring will have pink flowers. If, now, one of these plants with pink flowers is self-pollinated, or if pink-flowered plants are cross-pollinated, their offspring will consist of red-flowered, pink-flowered, and white-flowered plants in the proportion of one red, two pink, and one white. If, now, the red-flowered plants are self-fertilized, all their offspring will have red flowers, and successive generations will continue to have red flowers for as many generations as they are self-fertilized. In the same way, if the white-flowered plants are self-fertilized, their offspring will have



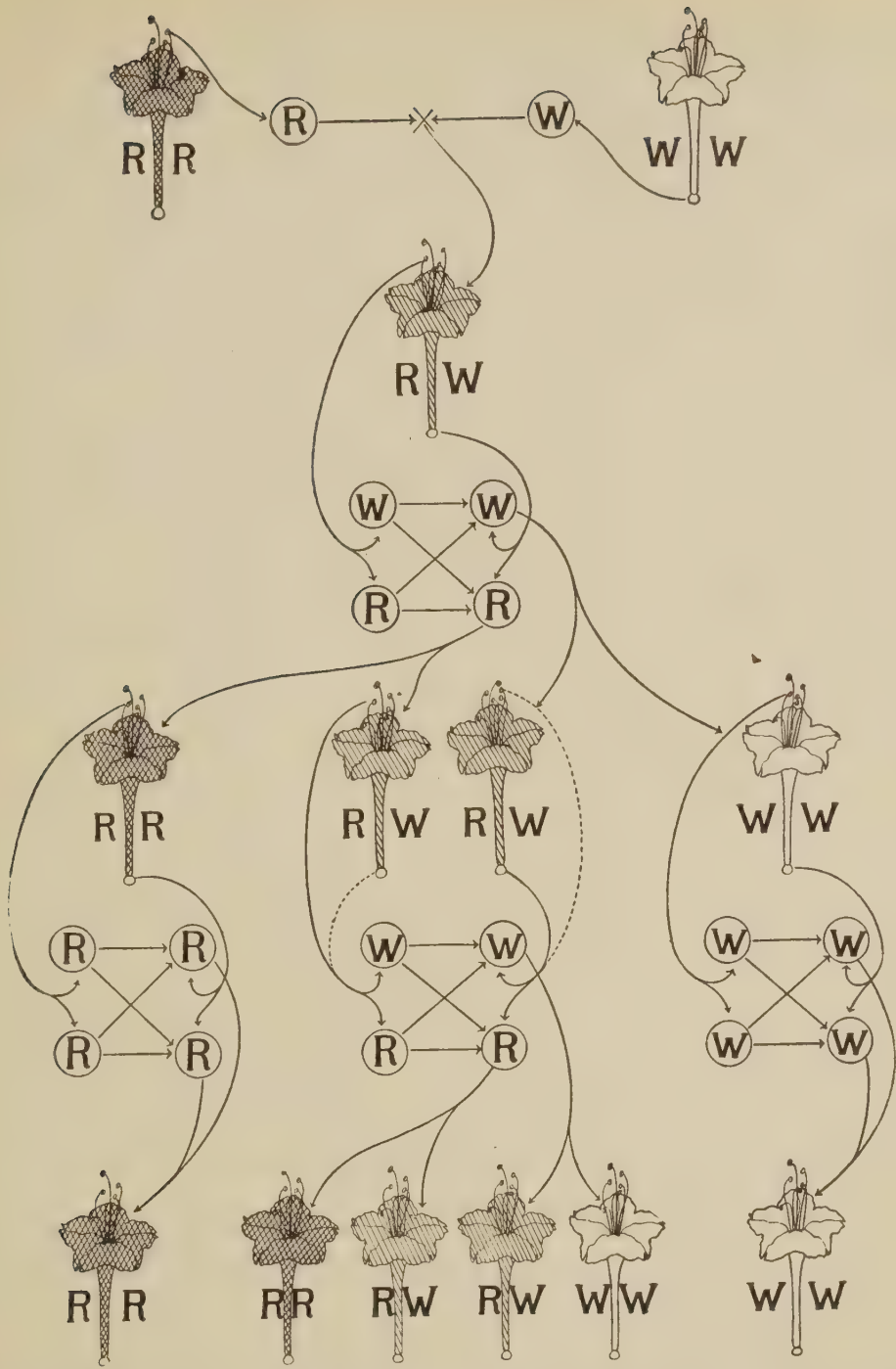


FIG. 232. Diagrammatic representation of inheritance of flower color in four-o'clock

The flowers represent individuals: cross hatching, red; single hatching, pink; unshaded, white. The letter *R* represents a factor for red; *W*, a factor for white. Rings signify gametes; straight lines represent union of sperm and egg; curved lines, the production of offspring

white flowers. When, however, pink-flowered plants are self-fertilized, they will, like their pink-flowered parents, again produce red-flowered, pink-flowered, and white-flowered plants in the ratio of one red, two pink, and one white. The inheritance of the flower color in this plant, and its explanation in terms of *factors* and chromosomes, is shown in Fig. 232. The flowers represent plants; *R*, a chromosome carrying a factor for red; *W*, a chromosome with a factor for white. Circles represent *gametes* (sexual cells).

The explanation of color inheritance in the four-o'clock is as follows: A red-flowered plant has two chromosomes, each with a factor for red. During the reduction division these segregate so that the gametes possess only a single chromosome with a factor for red. Likewise, a white-flowered plant has two factors for white, while a gamete produced by a white-flowered plant carries only one such factor (line 1, Fig. 232).

The hybrid (known as the  $F_1$ , or first filial, generation) is therefore produced by the union of a gamete with a chromosome carrying a factor for red and a gamete having a chromosome with a factor for white. The result is that the hybrid possesses both a factor for red and one for white, and is pink-flowered (line 2, Fig. 232). When this individual gives rise to gametes, these will be of two kinds, some with a chromosome bearing a factor for red and others with a chromosome bearing a factor for white. Just as the chromosome carrying the factor for red and that with the factor for white came together in the fertilized egg, so they again separate before the formation of gametes. The generation ( $F_2$ ) formed as a result of the union of the gametes produced by the  $F_1$  hybrids is shown in Fig. 232. If a male nucleus with the factor for red fertilizes an egg with the factor for red, the result will be a plant which has two factors for red in all its vegetative cells and which will produce red flowers. Likewise, if a male nucleus with a factor for white fertilizes an egg with a factor for white, the fertilized egg will have two factors for white and the plant will produce white flowers. When, however, a male nucleus with a factor for white



fertilizes an egg which has a factor for red, or vice versa, the fertilized egg has a single factor for white and a single factor for red, and the resulting plant will have pink flowers. When the  $F_1$  hybrid gives rise to sexual nuclei, there will be, on the average, an equal number of egg nuclei with the factor for red and egg nuclei with the factor for white. Likewise, there will be an equal number of pollen grains with the factor for red and pollen grains with the factor for white. The two kinds of male nuclei produced will, according to chance, fertilize an equal number of eggs. Moreover, each kind of male nucleus will tend to fertilize an equal number of eggs with the factor for red and eggs with the factor for white. The male nuclei with the factor for red will then fertilize eggs in the ratio of one with the factor for red to one with the factor for white, so that there will be one plant with red flowers to one with pink flowers. In a similar way, the male nuclei with the factor for white will give rise to one plant with pink flowers to one plant with white flowers. Thus we get plants in the ratio of one plant with red flowers, two with pink, and one with white (Fig. 232).

**Purity of gametes.** Inheritance of color in the four-o'clock illustrates one of the fundamental principles of Mendelian inheritance, that is, *purity of gametes*. The fusion of two gametes with alternative characters, such as red and white, results in a hybrid the body cells of which will contain the factors for both characters. When, however, this plant produces gametes, the factors for these two characters will separate, and one of them will be found in one gamete and the other in another gamete. One gamete will thus contain only one of two such alternative characters. In other words, a gamete of a four-o'clock can contain either a factor for red or a factor for white, but not both. In this way the alternative characters are segregated when gametes are formed, so that no gamete is a hybrid so far as a single pair of characters is concerned. The segregation of the factors is due to their being located in corresponding chromosomes which are separated and distributed to different nuclei during the reduction division.

**Definition of terms.** In discussing heredity there are a few technical terms which are very convenient and which are used in even the simplest discussions of the subject. A few of these are here defined.

A *gamete* is a cell that fuses in sexual reproduction. A *zygote* is a cell formed as the result of sexual fusion. Two alternative characters, such as tallness and dwarfness, are known as *allelomorphs*. An individual is said to be *homozygous* for a certain character when it contains two factors for that character and does not contain the factor for the other member of the pair of allelomorphs. An individual is said to be *heterozygous* when it contains factors for both members of a pair of allelomorphs. When two plants are crossed, the parent plants are known as the  $P_1$  generation, and the resulting offspring as the  $F_1$  generation; when this generation is self-fertilized or interbred, the offspring compose the  $F_2$  generation; the subsequent generation is known as the  $F_3$  generation; etc.

**Dominance.** Mendel crossed tall and dwarf varieties of garden peas and found that their offspring in the first generation were all tall. These may be called tall hybrids, as they were produced by crossing tall and dwarf varieties. When these tall hybrids were self-fertilized, they gave rise to tall and dwarf plants in the ratio of three tall ones to one dwarf. When the resulting dwarf plants were self-pollinated, they always produced dwarf offspring. One third of the tall ones contained two factors for tallness and none for dwarfness, and when self-fertilized always gave rise to tall offspring only, while the other two thirds, which were tall hybrids, produced dwarf and tall, as did their hybrid parents, in the ratio of one dwarf to three tall. These tall plants, like those of the preceding generation, consisted of one third which had no factor for dwarfness and always gave rise to tall plants when self-pollinated, and two thirds which were tall hybrids and again repeated the ratio of three tall to one dwarf. This relation is shown in Fig. 233. The inheritance of the factors for tallness and dwarfness after the crossing of tall and dwarf plants is shown by the letters under the words



describing the heights of the plants.  $T$  represents tallness;  $D$ , dwarfness; and  $(D)$ , dwarfness which is dominated by tallness.

In the case just discussed, when tall plants were crossed with dwarf ones, their offspring were all tall. If plants with two opposite characters are crossed and their offspring show one of the characters and no influence of the other, then the character which appears in the offspring is said to dominate, or to be a

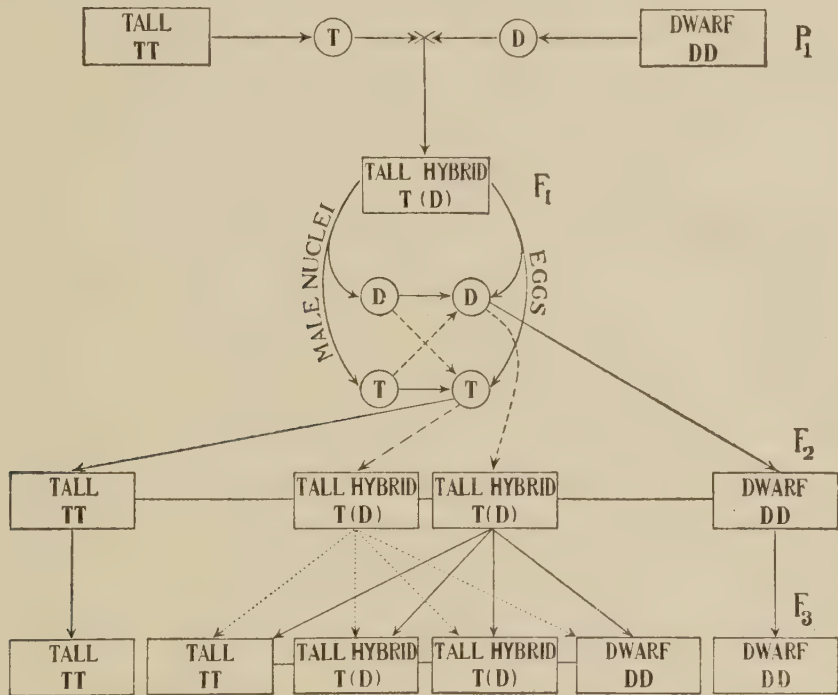


FIG. 233. Diagram showing inheritance of tall and dwarf characters in peas; also inheritance of factors for tallness  $T$  and dwarfness  $D$ . ( $D$ ) signifies dwarfness dominated by tallness

*dominant* character. A character which does not appear is said to recede, or to be a *recessive* character. In this case tallness is a dominant character as compared with dwarfness. *Dominance*, like purity of gametes, is an important Mendelian principle. In the case of the four-o'clock plants the red color of the flowers is not nearly so dominant as is tallness in peas. The red color of the four-o'clock is said to be incompletely dominant.

In different cases there may be various degrees of dominance. In some plants flower color may be just as dominant as tallness in peas, while in other plants length may be only partially

dominant. Thus, the fact that a character is dominant in one species does not necessarily imply that it is dominant in other species. Such facts can be determined only by observation.

On examining Fig. 233 we find that the factors for tallness and dwarfness are inherited in exactly the same way as the factors for color in four-o'clock plants. When a pure strain of tall peas is crossed with a dwarf one, the plants of the first hybrid generation contain a factor for tallness and also a factor for dwarfness, even though the factor for dwarfness is recessive. These plants, if self-pollinated, will produce three kinds of plants, even though, on superficial examination, there would appear to be only two. The three kinds are produced in a ratio of one which has two factors for tallness and none for dwarfness, and so can produce only tall offspring; two which contain both the factor for tallness and the factor for dwarfness, and so can produce both tall and dwarf offspring; and one which contains two factors for dwarfness and none for tallness, and so can produce only dwarf offspring. The plants which contain both the factor for tallness and the factor for dwarfness will be like their hybrid parents in hereditary height factors, and so will naturally give rise to the same kinds of plants as did their parents, and in the same proportion.

In writing the abbreviations of characters it is very convenient as well as customary to represent the dominant character by a capital letter, as *T* for tallness, and the recessive character by the same letter not written as a capital. Thus, when tallness is dominant over dwarfness, dwarfness may be indicated by *t*.

**Inheritance of two pairs of characters.** When we observe any organism we see that it is a morphological and physiological unit. From the standpoint of inheritance it is, however, made up of a number of hereditary units or characters, which most often appear to be inherited independently of each other. The examples of inheritance which we have considered demonstrate very clearly the segregation of characters and the purity of gametes, while the inheritance of height in peas is a good example of dominance. The independence of characters can be



emphasized by a consideration of the inheritance of two pairs of characters which Mendel studied in garden peas.

In peas round seed is dominant over wrinkled seed, and yellow seed over green seed. When, therefore, we cross a plant

having round yellow seed with one having wrinkled green seed, the  $F_1$  generation will have round yellow seed. If these hybrids are self-fertilized, they will give rise to the following kinds of plants in the following ratio: nine with round yellow seed, three with round green seed, three with wrinkled yellow seed, and one with wrinkled green seed. This relationship is shown in Fig. 234, in which the small squares represent individuals, while circles represent gametes.  $R$  stands for a factor for round;  $r$ , for wrinkled;  $Y$ , for yellow; and  $y$ , for green.

From the diagram it will be seen that the  $F_1$  generation contains a factor for round, one for wrinkled, one for yellow, and one for green. When this plant forms gametes, both the male and the female gametes will show four different combinations of factors: namely, round and yellow, round and green, wrinkled and yellow, and wrinkled and green. A male nucleus with the factors

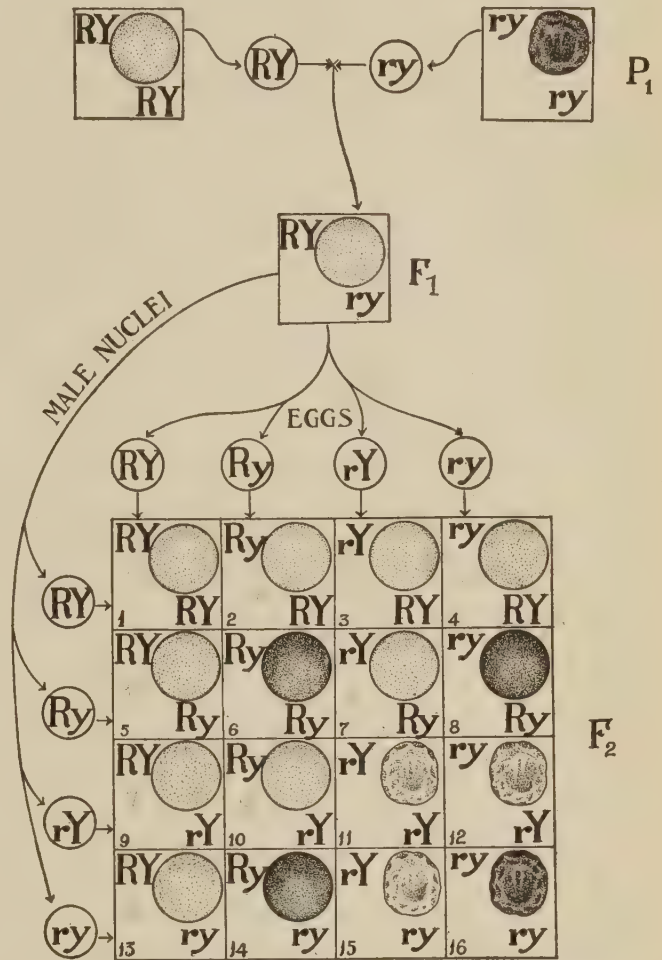


FIG. 234. Diagram showing inheritance of seed characters in garden peas

Squares represent individuals; circles containing letters are gametes; letters represent factors as follows:  $R$ , round;  $r$ , wrinkled;  $Y$ , yellow;  $y$ , green

for round and yellow can fertilize any of the four kinds of eggs, and according to chance will fertilize the different kinds in equal numbers. Likewise the three other kinds of male nuclei will fertilize all four kinds of eggs in equal numbers. The different combinations produced are shown in rectangles in the lower part of the diagram. Such a set of rectangles may be very simply constructed by writing the factors for one of the kinds of eggs in each square of the first vertical row of squares, and the factors for each of the other kinds of eggs in a separate vertical row of squares. The characters for male nuclei should be similarly written in horizontal rows. If we examine the squares in the lower part of the diagram, we shall see that there are nine which contain both *R* and *Y*, and so represent plants with round yellow seed; three which contain *R* but not *Y*, and so represent plants with round green seed; three which contain *Y* but not *R*, and so represent plants with wrinkled yellow seed; and one square which contains neither *R* nor *Y*, and so represents a plant with wrinkled green seed. The last-mentioned rectangle is the only one of the sixteen which represents a plant that is pure for both recessive characters. Likewise, there is only one of the sixteen rectangles which represents a plant that is pure for both dominant characters.

A line drawn diagonally from the upper left-hand corner to the lower right-hand corner of the large square in the lower part of Fig. 234 passes through four small squares, each of which represents a different kind of individual that is homozygous for one of each of the two pairs of characters. Similarly, a line drawn from the lower left-hand corner to the upper right-hand corner of the large square passes through four small squares, each of which is heterozygous for both pairs of characters.

The  $F_2$  generation of a cross between peas having round yellow seed and peas having wrinkled green seed shows very clearly that in this case the pairs of characters are independent of each other. In other words, round and yellow, and likewise wrinkled and green, are inherited independently of each other.



**Linkage.** The number of chromosomes in an organism is usually not very great, while, on the other hand, the organism has a large number of characters. It should follow from this that one chromosome would carry several or many different factors. Moreover, factors which are in the same chromosomes should be linked together in inheritance. This reasoning is borne out by the fact that many characters are linked together in inheritance. In the Chinese primrose the factors for red stigma, red flower color, long style, dark stem, and light corolla tube are linked together. In garden peas the factor for round seed as opposed to wrinkled seed and the factor for tendriled as opposed to nontendriled leaves go together. We may conclude, therefore, that factors in the same chromosome are linked together, while those in different chromosomes are independent.

**Trihybrids.** In the consideration of the inheritance of two pairs of characters we have seen that sixteen combinations are involved in the  $F_2$  generation. These include plants of four different appearances and nine different germinal compositions. When three pairs of characters are considered, sixty-four individuals are involved in the  $F_2$  generation. These include plants of eight different appearances and twenty-seven different germinal compositions. Only one of the sixty-four contains only dominant factors, and, likewise, only one contains only recessive characters.

The inheritance of three pairs of characters may be illustrated by garden peas. In these plants we have seen that tallness is dominant over dwarfness, yellow seed is dominant over green seed, and round seed is dominant over wrinkled seed. If tall individuals with yellow round seed are crossed with dwarf ones with green wrinkled seed, the offspring in the  $F_1$  generation will contain factors for tallness, dwarfness, yellow, green, round, and wrinkled; but all the individuals will be tall with yellow round seeds, as these characters are dominant.

When the  $F_1$  generation forms gametes, these are of eight kinds, and the fusing of eight kinds of eggs with eight kinds of male nuclei gives rise to sixty-four combinations. These

relationships are shown in Fig. 235, in which *T* represents tall; *t*, dwarf; *Y*, yellow; *y*, green; *R*, round; and *r*, wrinkled.

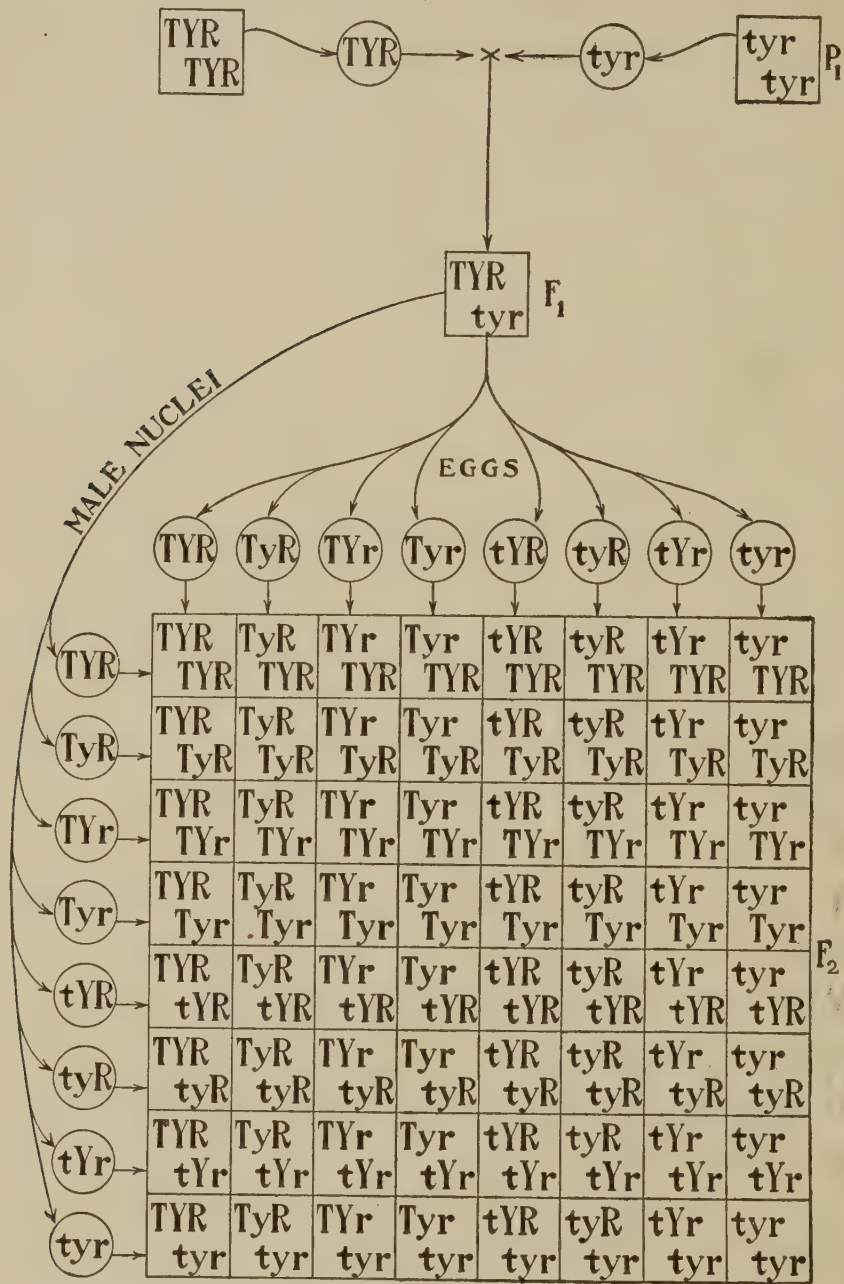


FIG. 235. Diagram showing inheritance of three pairs of characters in garden peas: tallness, *T*, dominant over dwarfness, *t*; yellow seed, *Y*, dominant over green seed, *y*; round seed, *R*, dominant over wrinkled seed, *r*

**Complementary factors.** In all the cases that we have so far considered, a single factor is responsible for the production of a character, but in some cases more than one factor is necessary. This may be illustrated by the case of two strains of



white-grained corn which, when crossed, will give all red grains in the  $F_1$  generation. In the  $F_2$  generation there will be nine red to seven white. This ratio suggests at once that here is a case of the inheritance of two factors. In such a case nine out of sixteen individuals have both dominants of two pairs of allelomorphs.

Two factors were necessary to produce the red color, and one of these was present in one of the strains and the other in the other strain. When these two strains were crossed, all the individuals in the  $F_1$  generation contained both factors and so were red. In the  $F_2$  generation nine of the sixteen individuals contained both factors that were necessary for color and so were red, six contained one or the other of the two factors and were white, while one did not contain either of the two factors and so was white. Two factors, both of which are necessary for the production of a single character, are known as complementary factors.

The inheritance of the factors in the above case is shown in Fig. 236, in which one of the necessary factors is represented

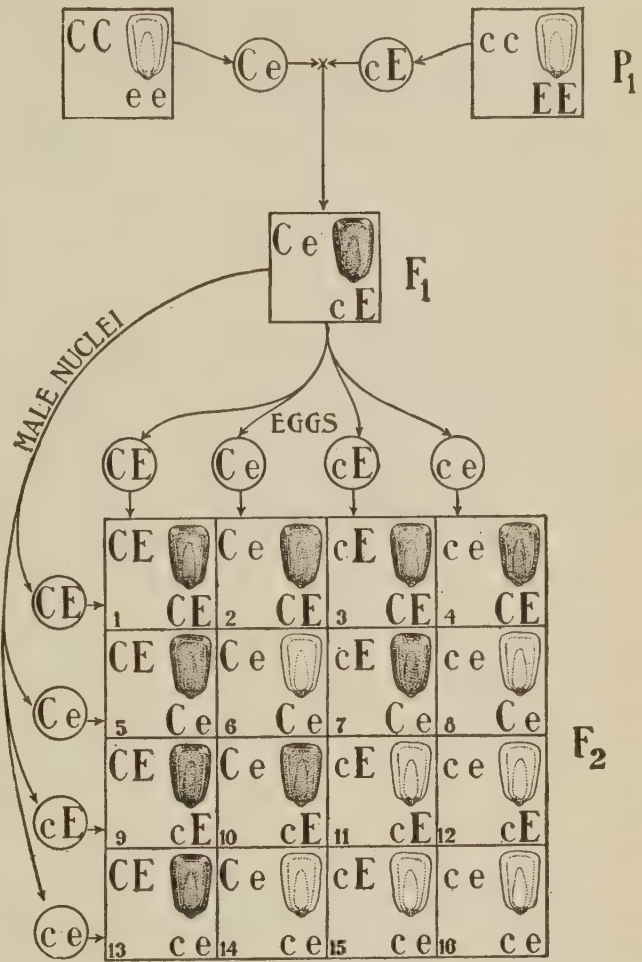


FIG. 236. Diagram of inheritance of complementary factors producing a red color in corn

The complementary factors are dominant and are represented by  $C$  and  $E$ , while their absence is shown by  $c$  and  $e$  respectively. Each parent has only one of the complementary factors and is white, while the  $F_1$  hybrid has both factors and is red. The red color in the grain is indicated by stippling

as  $C$  and its absence as  $c$ , while the other is represented as  $E$  and its absence as  $e$ .

Many pigments in plants are produced by the action of *enzymes* on a colorless substance, known as *chromogen*. What may be the explanation of the above case of inheritance in corn is that one of the strains of white-grained corn contained a factor for chromogen and the other a factor for an enzyme capable of acting on the chromogen and producing red. When these two strains were crossed, the resulting plants contained both chromogen and enzyme, and so the grains were red.

A consideration of complementary factors shows that more than one factor may be necessary to produce a given character, and it is probable that any character is the result of several or many factors. When the inheritance of a pair of contrasting characters appears to be due to a single pair of factors, this does not mean that only one factor is necessary for the production of a character, but simply that a difference between two factors of a pair results in the appearance of a pair of contrasting characters. In the case of the inheritance of red color in corn, illustrated in Fig. 236, the color is due to at least two factors. However, if we were to cross the individuals represented by squares 1 and 6 in the lower part of the diagram, red would appear to be a simple Mendelian dominant, conditioned by a single factor, as the two individuals differ from each other only in the factors  $E$  and  $e$ . Not only is one character the result of the interaction of many factors, but one factor may influence more than one character.

**Cumulative factors.** Some plants contain more than one pair of factors which produce similar results. Such factors are known as cumulative factors. These may be illustrated by certain strains of wheat. In breeding experiments a strain of wheat with white kernels was crossed with one with red kernels, and the individuals of the  $F_1$  generation were intermediate in color. In the  $F_2$  generation there were fifteen red to one white. Moreover, the red individuals were represented by four shades of red. The explanation of the results is that the red strain contained two pairs of factors for the production of red, that



the different factors were cumulative in their action, and that all four factors were necessary for the production of the depth of color shown by the parent red strain. If we let  $A$  stand for one of these factors for red, and  $B$  for the other factor, then the red strain may be represented by  $AABB$ , and the white strain by  $aabb$ . When these two strains were crossed, the  $F_1$  generation contained the factors  $AaBb$ . The individuals of this generation thus contained only half as many factors for red as the parent red strain, and their color was intermediate between that of the red and the white strain. When this  $F_1$  generation formed gametes, they were of four kinds,  $AB$ ,  $Ab$ ,  $aB$ , and  $ab$ .

The  $F_2$  generation should therefore show the sixteen combinations characteristic of dihybrids. Fig. 237 shows the results. An examination of the squares in the lower part of the diagram shows that only one out of sixteen does not contain either  $A$  or  $B$ . This individual has only recessive characters and is white, while the other fifteen are red. Only one, however, contains four factors for red, and this is the only one with as deep a

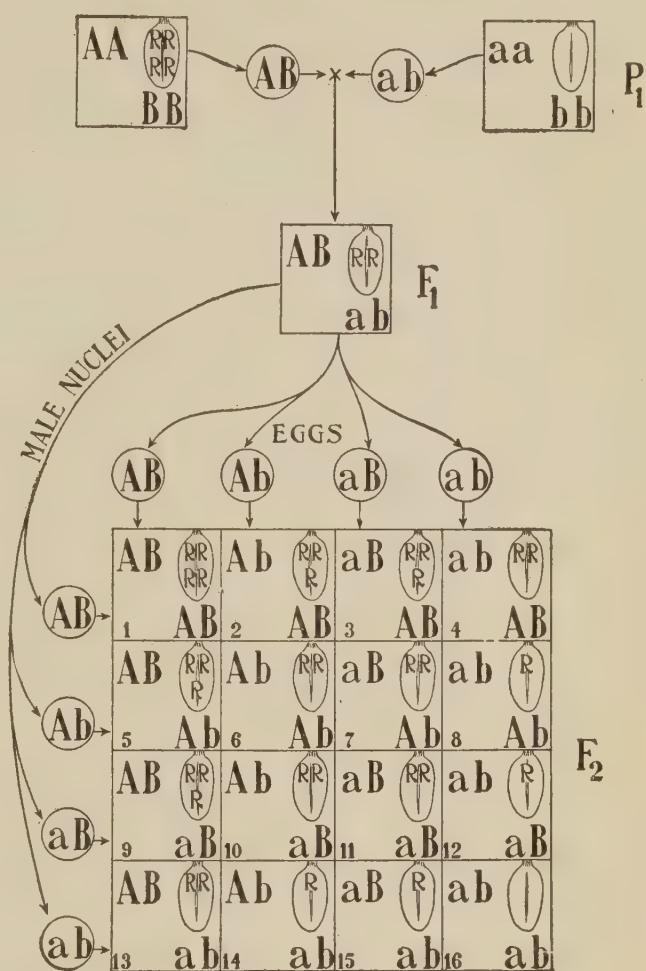


FIG. 237. Diagram representing inheritance of two pairs of cumulative factors,  $AA$  and  $BB$ , which produce a red color in wheat

The absence of  $A$  and  $B$  is represented by  $a$  and  $b$  respectively. Squares represent individuals; circles, gametes. The number of factors for red, and consequently the degree of redness, is shown by the number of the letters  $R$  in the wheat grains.

shows that only one out of sixteen does not contain either  $A$  or  $B$ . This individual has only recessive characters and is white, while the other fifteen are red. Only one, however, contains four factors for red, and this is the only one with as deep a

color as the original red strain. Six individuals contain two factors for red, or exactly half the number in the original red strain. The number of factors for red (and so the depth of color) is indicated by the number of the letters *R* shown in the grains in the squares.

Another set of experiments with wheat is even more interesting in connection with cumulative factors. A different red strain was crossed with a white strain, and the individuals of the  $F_1$  generation were again intermediate in color. In the  $F_2$  generation there were sixty-three reds of various shades to one white. In this case the red strain appeared to contain three pairs of factors for red, all of which seemed to produce about the same degree of color and all of which were necessary to produce the depth of color shown by this strain. The proportion of sixty-three red to one white is evidently a trihybrid ratio. In trihybrid ratios there is only one out of sixty-four in the  $F_2$  generation which is purely recessive, and so, if the red strain contained three pairs of factors for red, the  $F_2$  generation of a cross between this red and a white should produce only one out of sixty-four individuals without a factor for red. Likewise, there would be only one out of sixty-four which would have six factors for red and which would be as dark as the red strain. In all there were six degrees of redness.

In some cases crosses are made in which offspring intermediate in characters appear to breed more or less true to the type of the  $F_1$  generation. It is interesting to consider these cases in connection with cumulative factors. If there were six pairs of cumulative factors, then in the  $F_2$  generation each of the original types would be represented by only one individual out of 4096. The  $F_1$  generation would be intermediate in characters between the two parent forms, and in subsequent generations it would be very rare to find an individual like either of the parent types; unless very large numbers of individuals were reared, such types might fail altogether to appear. The hybrid would then seem to breed more or less true to the hybrid type.



**Application of Mendelism.** The laws of inheritance known as Mendelism were first discovered in plants. Afterward they were found equally applicable to animals, as well as to human beings. The value of definite laws which can be applied to animal and plant breeding can hardly be overestimated, while human society seems certain to be profoundly influenced by the application to itself of these same laws.

Much greater progress has been made in the study of Mendelism in plants and animals than in man, as it is of course not possible to conduct experiments with human beings in the same way as with plants and animals. Moreover, we know that most human beings are very complex hybrids, and this in itself makes it difficult to study inheritance in man. Also, man is a slow-breeding animal, so that it has been impossible for modern students of heredity to observe many generations, while it is difficult to get accurate descriptions of characteristics of generations that have died.

Many human characters which seem to behave in Mendelian fashion have been catalogued. Among these are curly hair dominant over straight hair, dark hair over light hair, brown eyes over blue eyes, normal pigmentation over albinism, and normal condition over hereditary insanity or feeble-mindedness. In crosses between the negro and the white, color of skin does not act as a simple character dependent on one factor. In the  $F_2$  and subsequent generations, however, there may be individuals much lighter or much darker in color than the mulatto parents. Indeed, the color may be as dark as that of a negro or light enough to pass for white. These results indicate that the color is conditioned by multiple factors which act in Mendelian fashion. In a previous connection we have seen that if three cumulative factors are concerned, then in the  $F_2$  generation each of the original races would be represented by only one individual out of sixty-four, while sixty-two would be intermediate. If six factors were concerned, only one out of 4096 individuals of the  $F_2$  generation would have the germinal composition of each original race.

## PLANT BREEDING

**Selection.** The method of obtaining improved varieties has been that of selecting plants with desired characters for propagation, and discarding undesirable ones. Of course, the act of selecting individuals with desirable characters cannot produce anything new, as selection presupposes variations which can be selected. In order to learn how new varieties are produced it is necessary, therefore, to consider the origin of variation. *Variation* is a universal phenomenon among both plants and animals, — so universal, in fact, that it has given rise to the common expression that no two plants or animals are alike.

**Acquired characters.** Favorable methods of cultivation frequently result in the production of larger and more vigorous individuals. If a plant attains to an exceptionally large size by growing under unusually favorable conditions, this size is said to be an acquired character, as it is one acquired during the life of the individual and not one that the individual inherited. Such acquired characters do not appear to be inherited. The seeds of vigorous plants are likely to be larger than those of weak plants; large seeds contain more stored food than smaller ones, and so give the seedlings a better start. In this way the offspring of a vigorous plant may be somewhat larger than the offspring of a less vigorous one. This character, however, is not hereditary, as the larger size will be maintained only so long as each generation is grown under the favorable conditions that gave rise to this exceptional vigor.

**Continuous variations.** The variations between plants are of different kinds. Some are minor variations, known as continuous variations, which are not inherited. When many plants of one homozygous variety are examined, it is found that they differ from one another by slight variations which are quantitative in character and do not depart from the average beyond a certain limit. Thus, some plants will be shorter and others taller, some will have deeper-colored and others lighter-colored flowers, etc. While the plants of one generation may vary thus



among themselves, the average for large numbers will be constant for different generations. Continuous variations are largely or entirely due to environmental conditions. They are said to be continuous because between any two variations there is a gradual series of variations which differ from one another by imperceptible gradations. Continuous variations are also called fluctuating variations, because in successive generations the character fluctuates around the same average.

The selection of fluctuating variations cannot produce varieties with different hereditary characteristics, because, when an extreme type is selected, the progeny always tend to return to the average. The most that can be accomplished by selecting such variations is to produce a quantitative change while the selection is continued. If, during several succeeding generations, the seeds of the tallest plants of a variety are selected for propagation, we may get taller plants than the average, but this extra height will disappear as soon as selection is discontinued.

**Hybrids.** Hybrids are the offspring produced by the union of the sexual cells of different genera, species, or varieties. The offspring resulting from the crossing of white-flowered and red-flowered plants of the same species are examples of hybrids, as are also the offspring obtained by crossing different genera, as the radish and the cabbage. In general, crosses are most easily made between closely related races. When the races are not closely related, the hybrids usually show a lessened fertility or absolute sterility, while hybrids formed by crossing distantly related species are frequently lacking in vigor.

**Variations due to hybridization.** When two varieties of plants which differ from each other in a number of characters are crossed, their offspring will usually show some of the characters of each parent, while those characters which are recessive and do not appear in the  $F_1$  generation will do so in subsequent generations. Hybridizing, therefore, tends to produce variations. A knowledge of the Mendelian laws of inheritance enables us to combine hybridizing and selecting much more intelligently than we could otherwise do. We have seen that a cross between

tall peas with round yellow seeds and dwarf peas with wrinkled green seeds gives, in the  $F_1$  generation, tall plants with round yellow seeds, as the characters tall, round, and yellow are dominant over the alternative characters. If it were desirable to have dwarf plants with round yellow seeds, these could be obtained in the  $F_2$  generation. In this generation one out of sixty-four individuals would be homozygous for dwarf, round, and yellow. The progeny of these individuals would therefore breed true. The  $F_2$  generation would also contain dwarf individuals with round yellow seeds which would not breed true. Such plants would be heterozygous for round or yellow or for both of these characters. In order to distinguish between the plants which are homozygous for the desired characters and those which are heterozygous it is only necessary to obtain a sufficient number of plants of the next generation and see which plants breed true. This example enables us to see how we can combine the desirable characters of one variety with those of another and get a variety that is superior to both of the parent varieties.

Mendelism also shows that certain characters are the result of a heterozygous condition, and that we cannot obtain a variety that will breed true for such characters. Pink four-o'clocks afford a good example. As pink flowers are produced only by heterozygous individuals, pink-flowered plants will never breed true but will produce red-flowered, pink-flowered, and white-flowered plants in the ratio of one, two, and one.

**Mutations.** It has been pointed out that the selection of continuous variations does not result in hereditary changes, while hybridization may produce new varieties. There are, however, variations which are not the result of hybridization and which are hereditary. These may occur even in pure lines, that is, in strains descended from a single self-fertilized homozygous individual. Such hereditary variations are much less numerous than are fluctuating variations, and are known as mutations. Characters which appear as the result of mutations are inherited in Mendelian fashion and may be either dominant or recessive. In popular language, mutations are frequently spoken of as sports.



The improvement of cultivated plants has frequently been due to the selection of mutations. Red sunflowers and giant varieties of tobacco are examples of mutations.

A character which results from a mutation may be considered as due to the modification of something already present rather than as the result of the addition of an entirely new factor. A mutant may vary greatly or only slightly from the parent.

The red sunflower affords a good example of a mutant. In the sunflower the so-called flower is, in reality, a head composed of many flowers packed close together. The central, or disk, flowers are small, while the outer, or ray, flowers are large and have a brilliant orange color. It is these ray flowers which are largely responsible for the attractive appearance of the head. In the year 1910 a sunflower with chestnut-red rays was found by a roadside in Boulder, Colorado. The plant was very striking, and its presence could only be explained as due to mutation. In order to reproduce the plant it was necessary to cross it with a plant having ordinary orange-colored rays, as sunflower plants are not fertile unless cross-pollinated. In the  $F_1$  generation of this cross about half the plants were red and the other half orange. Subsequently the red color proved to be a Mendelian dominant. Therefore the explanation of the fact that in the  $F_1$  generation of the original cross half the offspring showed the red color and half the orange color would seem to be that the original red mutant was heterozygous and contained only one factor for red.

An examination of the red color of the red sunflowers showed that the chestnut-red color was due to the fact that both a red pigment and the original orange pigment were present in the rays. By subsequent breeding, plants were obtained that had rays with the red and without the orange color. These flowers were wine red or old rose. The breeding was carried out in the following manner:

Since the year 1889 there has been in cultivation a variety of sunflower called primrose, which arose as a mutant from the ordinary orange variety and which is pale yellow. This variety was crossed with the chestnut red. In the  $F_1$  generation the offspring were all chestnut red, as the orange color dominates

the pale yellow and the red dominates the absence of red. In the  $F_2$  generation there were four kinds of plants obtained: chestnut red, orange, wine red, and light yellow.

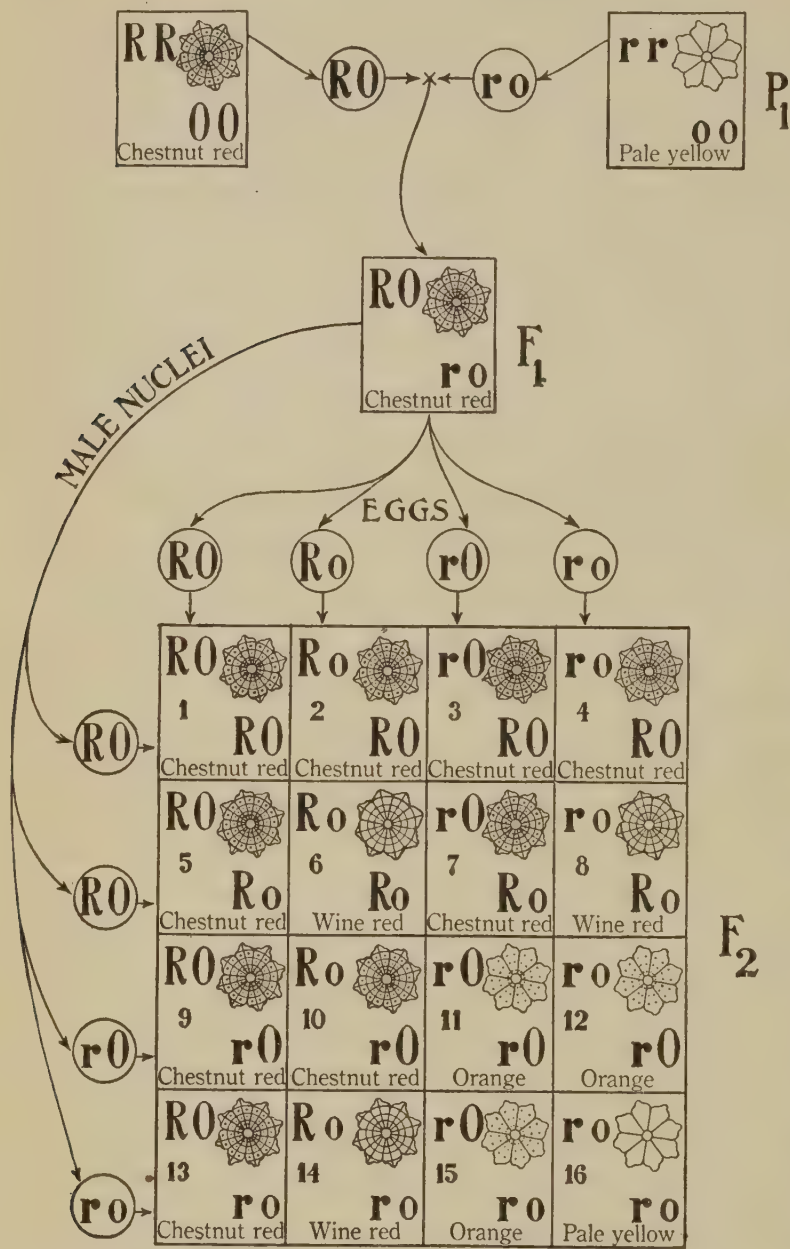


FIG. 238. Diagram of inheritance of flower color in sunflower

$R$  represents a factor for the dominant character red;  $r$ , the absence of this factor;  $O$ , the factor for the dominant color orange; and  $o$ , the factor for the recessive pale yellow.  $R$  and  $O$  together produce chestnut red

red, orange, wine red, and light yellow, approximately in the proportion of nine, three, three, one. This is the dihybrid ratio and shows that in this case we are considering two pairs of independent unit characters. The first pair is the dominant red,  $R$ , and the recessive, which is the absence of red,  $r$ ; the second pair is the dominant orange,  $O$ , and the recessive pale yellow,  $o$ . By means of these symbols there is shown, in Fig. 238, the crossing of the chestnut red and the light yellow and the composition of the  $F_1$  and  $F_2$  generations. In the case of the red sunflower we see

how a new variety can arise as a mutation, and how still other new varieties can be obtained by further breeding.



**Hybrid vigor.** The crossing of two races which are not too distantly related frequently results in an increased vigor, known as hybrid vigor, in the offspring (Fig. 239). In wide crosses there is often an increased vigor accompanied by sterility, as in the well-known case of the mule; in very wide crosses sterility may be accompanied by a lessened vigor; while if the germinal composition of two races is too dissimilar, it is impossible to hybridize them.

Within the range in which crossing results in an increased vigor without lessened fertility, the vigor increases with the degree of

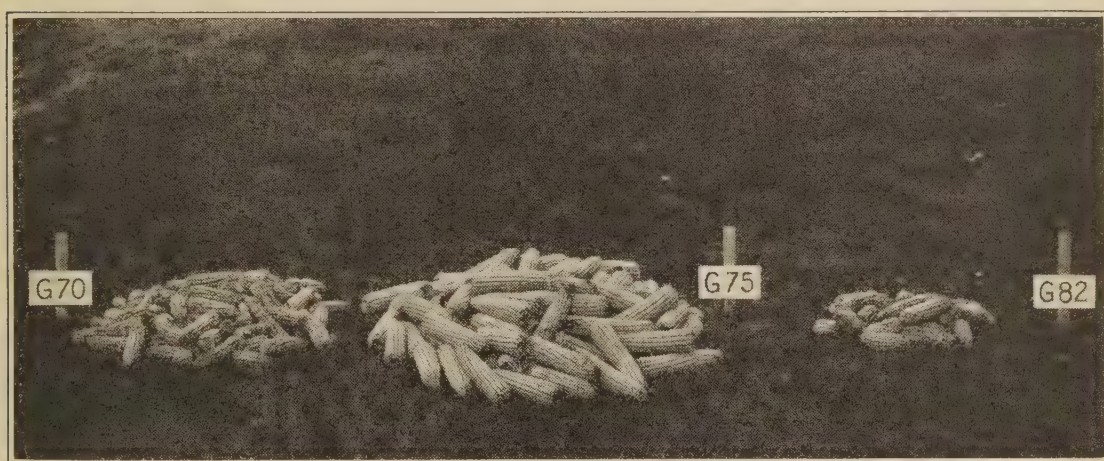


FIG. 239. Hybrid vigor in corn

Right and left, two inbred strains; center, their  $F_1$  progeny

heterozygousness resulting from the cross. Self-fertilization of a heterozygous race results in a decrease in the heterozygous condition; and so, as might be expected, self-fertilization of a vigorous hybrid race results in a decrease in vigor which continues until a homozygous condition is reached, after which there is no further deterioration.

Hybrid vigor appears to be connected with the fact that the hybrid contains the dominant factors of both parents, and that, usually, dominant characters are desirable and promote vigor.

Likewise, the deterioration which follows the self-fertilization of vigorous hybrids seems to be connected with a decrease in the number of dominant factors in the homozygous races. Moreover, when a large number of contrasting factors are involved, the

linkage of factors in the same chromosome prevents the accumulation in a homozygous condition of all the dominant factors present in the hybrid. Thus, if a chromosome from one parent of the hybrid contained the dominant factors *A* and *B* and the recessive factors *c* and *d*, and the corresponding chromosome from the other parent carried the recessive factors *a* and *b* and the dominant factors *C* and *D*, the hybrid would possess all four dominant factors; but it is not to be expected that self-fertilization would result in an individual homozygous for the four factors, *A*, *B*, *C*, and *D*.

**Inbreeding and outbreeding.** Self-fertilization, or the crossing of closely related individuals such as brothers and sisters or parent and offspring, is known as inbreeding, while the crossing of unrelated individuals is known as outbreeding.

**Inbreeding.** The majority of flowering plants are provided with some device for promoting cross-pollination. On the other hand, some vigorous plants, such as wheat, rice, barley, oats, tobacco, beans, and tomatoes, are characterized by very nearly continuous self-fertilization. Self-fertilization in these cases certainly does not appear to be harmful. Therefore we may conclude not only that cross-fertilization is not always necessary, but also that self-fertilization is not necessarily harmful.

It would seem that continuous vegetative propagation without any sexual reproduction is also without deleterious effects. Ordinary varieties of bananas and pineapples are examples of very vigorous plants that are always reproduced vegetatively. Moreover, they have reproduced in this manner throughout the whole period during which we have knowledge of them. As far as hereditary composition is concerned, vegetative reproduction and self-fertilization of homozygous strains should have the same effect.

**Self-fertilization in corn.** Vigorous varieties of corn have been found to be complex hybrids. Self-fertilization of such varieties results in rapid deterioration. This deterioration is most marked in the  $F_1$  generation. The deterioration continues for several succeeding generations, but the amount of deterioration becomes less and less. The final result is the production



of approximately homozygous strains which differ greatly from each other. When, as a result of self-fertilization, the strains become homozygous, no further deleterious effects are produced by self-fertilization. When the deteriorated homozygous strains are crossed, the vigor of the original plants is restored (Fig. 239). This result shows that the deleterious effects following self-fertilization were the result of reducing the plants to a homozygous condition. Crossing the deteriorated strains restored the heterozygous condition, in which the unfavorable recessive characters were again masked by favorable ones.

**Deleterious effects of inbreeding.** If a strain contained no unfavorable recessive characters, self-fertilization could not cause the appearance of any such characters. The valuable strains in such self-fertilized plants as wheat and beans appear to be homozygous, and self-fertilization cannot produce deterioration by permitting the appearance of unfavorable recessive characters. We may conclude, therefore, that self-fertilization can produce no harmful effect in homozygous strains, but that it can do so in strains which are heterozygous, as it decreases the number of dominant factors and allows unfavorable characters to appear. It is apparently for this reason that harmful results frequently follow the close mating of domestic animals and of man. These are usually complex hybrids and frequently carry unfavorable recessive factors which are masked by favorable dominant ones.

The crossing of two separate individuals, which is characteristic of cross-pollinated plants and of all higher animals, has a tendency to promote a heterozygous condition, and an increase in heterozygousness is frequently associated with increased vigor. Self-fertilization, or close inbreeding, has a tendency to produce a homozygous condition, and so frequently results in decreased vigor in species that are normally cross-fertilized and heterozygous.

**The value of outbreeding.** Outbreeding frequently affords a great advantage over inbreeding in that it results in increased vigor, and also because it permits the combination of characters of different varieties. The vigor of the  $F_1$  generation of a cross

is frequently utilized in breeding. A conspicuous example is that of the mule, obtained by crossing a mare and a male ass. In plants many valuable hybrids are reproduced vegetatively by buds or by cuttings. This method of preserving a hybrid is very frequently practiced with fruit trees and ornamental plants.

While crossing different strains frequently results in increased vigor, it does not follow that a good variety will be improved by crossing with a poor one; in fact, the reverse is usually the case. It is, of course, not to be expected that a valuable variety can be improved by the incorporation of undesirable characters in it.

**Combination of outbreeding and inbreeding.** When a plant can be reproduced readily by vegetative means, it is a simple matter to retain the desirable characters found in a hybrid. The case is very different, however, with organisms that are reproduced only by the sexual process. In such cases, if a hybrid is heterozygous for many desirable characters, a strain that will breed true for a considerable proportion of them can frequently be obtained by inbreeding. Very valuable results may be produced by such inbreeding accompanied by vigorous selection.

#### NATURAL SELECTION

The method of improving cultivated plants has been that of selection, which may or may not have been accompanied by hybridization. Not only is selection the method of improvement but, moreover, continued selection is frequently necessary if the best qualities of cultivated plants are to be maintained. Naturally all injurious mutations should be eliminated, as should all undesirable individuals resulting from hybridization.

Since selection plays such a prominent part in the growing of cultivated plants and domestic animals, it is not surprising that in nature too plants and animals are subject to a process of selection. This selection by nature is called *natural selection*, to distinguish it from artificial selection, or selection by man.

**Struggle for existence.** Observation of natural conditions indicates very clearly that, except where man has interfered, a given



area contains about as many plants and animals as it can support. On the average, then, each plant produces one offspring which reaches maturity and takes the place of its parent. Every mature plant, however, produces many seeds, each of which contains a young plant. If all the seeds produced by one plant and its descendants should come to maturity, the descendants would soon be numerous enough to cover the earth. Likewise, if all the descendants of a pair of animals lived to old age, there would be enough of them to populate the earth in a short time. Natural selection results from the facts that a given region is fully occupied by plants and animals, that these give rise to many offspring, and that, owing to competition, only a small proportion of the offspring can grow up and in turn leave descendants.

Owing to the large number of offspring produced, there is necessarily competition between the offspring and also between these and their parent. There is competition not only between individuals of the same species but also between different species. This competition is the so-called struggle for existence. In the case of animals it is perhaps easier to visualize than in the case of plants. There is, however, just as true competition between plants as between animals. Every farmer knows that it is necessary to keep down the competition between weeds and his crop plants by destroying the weeds. Otherwise the weeds would be successful and the crops would disappear.

**Survival of the fittest.** In the competition between plants and between animals chance plays a considerable part. For example, many seeds never reach situations where it is possible for them to germinate. Nevertheless it is true that, in general, those individuals that are best adapted to their environment and for withstanding competition will survive. In other words, competition results in the survival of the fittest. By this we do not mean the survival of those which are more pleasing or more useful to mankind, but those which are best fitted to live under the conditions of their environment and to withstand competition. The survival of the fittest might just as well be termed "the elimination of the unfit," as what really happens is that the unfit are eliminated.

In natural selection it is those plants that are not fitted to their environment, or for withstanding competition, that are eliminated, while in artificial selection the plants that are discarded are those thought to be least serviceable to mankind. It frequently happens, therefore, that mutations which would be selected and thus preserved by man are very different from those which are preserved by natural selection. Such a mutation as a seedless orange is desirable from the standpoint of man but could not continue to exist in nature. From the standpoint of a plant subject to natural selection many seeds and a comparatively small amount of pulp are favorable characters.

In nature variegated leaves with white areas resulting from a lack of chlorophyll would be a disadvantage, as the material used in constructing these areas would be wasted as far as the chief function of the leaves is concerned. From the standpoint of artificial selection such plants are frequently desirable on account of their ornamental value. In nature such variegated leaves are very rare, but they are very common in cultivation.

Under natural conditions any mutation the result of which is unfavorable to the preservation of the species will be eliminated by natural selection, but there is a tendency for favorable mutations to be preserved.

From the foregoing discussion it is easy to understand why many of our cultivated plants cannot survive when left to themselves. Also, it is evident why plants seem thoroughly adapted to their environment.

**Significance of sexuality.** The value of sexuality is a subject about which there has been much dispute. All species of higher animals are composed of males and females. This results in the production of only half as many offspring as there would be if the animals were bisexual or reproduced by a vegetative process. The great majority of seed plants also reproduce sexually. Moreover, most of them are fitted with some device to insure cross-pollination. Considering that plants are subject to a rigorous natural selection, and that still the majority reproduce sexually, it would seem that this method must afford a real advantage.



Yet certainly neither cross-fertilization nor even a sexual process is necessary for successful reproduction. Among the lower animals there are bisexual species and also species in which the eggs develop without fertilization. Both of these types of animals seem vigorous and successful. There are numerous seed plants in which a sexual fusion is unknown and which produce fertile seeds. This may result either from the development of eggs without fertilization or from the growth of a vegetative cell into the embryo sac and its subsequent development into an embryo. As has been previously pointed out, plants which are reproduced vegetatively or which are habitually self-fertilized seem as vigorous as those that are reproduced sexually.

While the sexual process is thus not necessary for successful reproduction, this method does afford great advantage in the production of variations upon which natural selection can act. If a favorable mutation appeared in an individual of a species and another favorable mutation in another individual, these two mutations could be combined only as a result of the sexual process. One advantage of the sexual process would seem to be the production of new types of individuals which may be better fitted to survive.

## EVOLUTION

The production of anything by the process of gradual unfolding or gradual change is known as evolution. In this sense we speak of the evolution of a machine, the evolution of civilization, the evolution of a nation, the evolution of the world, or the evolution of the universe.

The present configuration of the earth is known to be due to the accumulation of the same kind of gradual changes as are going on around us at the present time. Streams gradually deepen their beds, while soil is washed from hillsides into rivers and then carried into lakes or seas. In this way the earth has become cut into ridges and valleys. In some places the land is rising, while in others it is sinking. Earthquakes and volcanic

eruptions also modify the geography of a locality. Changes such as those mentioned have evolved the present configuration of the earth's crust.

Plants and animals also undergo change; and a study of the origin of cultivated plants shows that most of the varieties have been produced by the selection of desirable variations. The wild species that inhabit the earth at present are also derived from previously existing plants. Such species are continually under the influence of natural selection. When a favorable mutation occurs in either a plant or an animal, there is a tendency for individuals having this mutation to persist at the expense of those without it. In this way the flora and fauna of the earth are gradually undergoing changes which tend to fit them better to their environment. This process is naturally a slow one. Animals and plants are already very thoroughly fitted to their environment, and it is not to be expected that changes which would make them more so would be conspicuous during the lifetime of one man.

The evolution of plants and animals, or the accumulation of the gradual changes which occur in them, is known as *organic evolution*.

**Organic evolution.** According to the theory, or law, of organic evolution the present floras and faunas of the world have been derived from those of past ages by gradual changes. During the course of these changes the organisms have, in general, become more complex and better fitted to their environment. The gradual process of evolution has, moreover, evolved plants and animals that are suited to very diverse environments. The original ancestors of present-day plants and animals must have been very simple indeed as compared with the most complex of their modern descendants.

The general similarity of protoplasm in physical structure, chemical composition, and physiological responses certainly indicates that all protoplasm came from the same source. Moreover, the similarity of the phenomena of sexuality and inheritance argues for a relationship of all higher animals and plants.



**Evidence of change.** Plants and animals at the present time undergo mutations, or, in other words, they change. This proves at once that organisms can change or undergo evolution. The only question that remains is to determine the extent to which they may evolve or have evolved. Fossil records, comparative morphology, and geographical distribution are probably the most important lines of evidence for evolution in plants; and one can realize the completeness of this evidence only after making a thorough study of these subjects. The evidence for evolution is not, however, confined to these, as all the fields of biology afford striking evidence. The more one knows of biology the more complete the evidence becomes.

**Comparative morphology.** A study of the many kinds of plants and animals shows that in both cases they range from single-celled individuals through many gradations to the most complex. Moreover, these different forms can be arranged in series which indicate that the more complex organisms have been derived from simpler ones. Indeed, this is true to such an extent that the only logical system of classification takes the form of a tree, indicating that the specialized forms came from more primitive groups, and these from still simpler ones, all pointing toward a common origin for the whole plant kingdom.

The most complex plants are characterized by having flowers and a complicated method of reproduction. Plants show many gradations, from single-celled plants without sexuality (Fig. 326) to the complex condition found in flowering plants. In some simple single-celled plants there is a fusion of similar cells; in such cases there is no differentiation of sex. In some slightly higher types the fusing cells are alike but are formed by many-celled individuals; such plants also have no differentiation of sex. Even some still higher types show only an indication of the differentiation of sex. Between the simplest plants with eggs and sperm and the flowering plants there are still many gradations of complexity in sexuality. This series will be treated in later chapters.

Just as there are gradations in the development of sexuality, so also there are gradations in vegetative complexity. There are

single-celled plants which not only lack sexuality but which do not have a well-defined nucleus, and in which the photosynthetic coloring matter is diffused through the protoplasm instead of being contained in special plastids (Fig. 312). In somewhat more highly developed types the whole plant consists of either a single cell or a group of similar cells with well-developed nuclei and chloroplasts. Between this simple vegetative structure and the differentiation characteristic of flowering plants there are many gradations. The various groups of plants will be considered in subsequent chapters.



FIG. 240. Leaves of a species of *Acacia*

On the left is the first leaf after the cotyledons; on the right, a somewhat older leaf in which the petiole is flattened and leaflike and takes the place of the leaflets. ( $\times 1$ )

In animals we find functionless structures which can best be explained on the ground that they have been inherited from ancestral forms in which they were of use. The human appendix is a well-known example. In human beings this structure is rudimentary and apparently serves no useful purpose, while in some lower animals it is a well-developed and useful organ.

The water plants from which the present land plants appear to have developed have motile sperms which swim in the water. Such motile sperms are possessed also by the simpler of the land plants, such as ferns and mosses. The simplest seed plants likewise have motile sperms, although these plants are fertilized by pollen tubes in much the same way as are flowering plants (Fig. 468). The presence of motile organs on the sperms of these seed plants can be explained best by assuming that these organs were derived from aquatic ancestors.

In the embryology of many animals, and to a less extent in the development of certain plants, there are characters which disappear in the adult and which resemble characters of more primitive ancestors. For example, ordinary leaves occur on the seedlings



of some plants the older individuals of which have highly specialized leaves (Fig. 240), indicating that these plants with highly specialized leaves have been derived from ancestors with ordinary leaves and that in their development they pass through a stage resembling the adult condition of those ancestors.

**Geographical distribution.** The present distribution of plants and animals can be explained only in the light of evolution.

Many plants have excellent means of seed dispersal and are very widely distributed. Frequently these are recent and very successful species and give us little or no insight into the past history of plants. In general, however, high mountains or seas impose barriers which many plants and animals cannot cross very readily if at all. Such

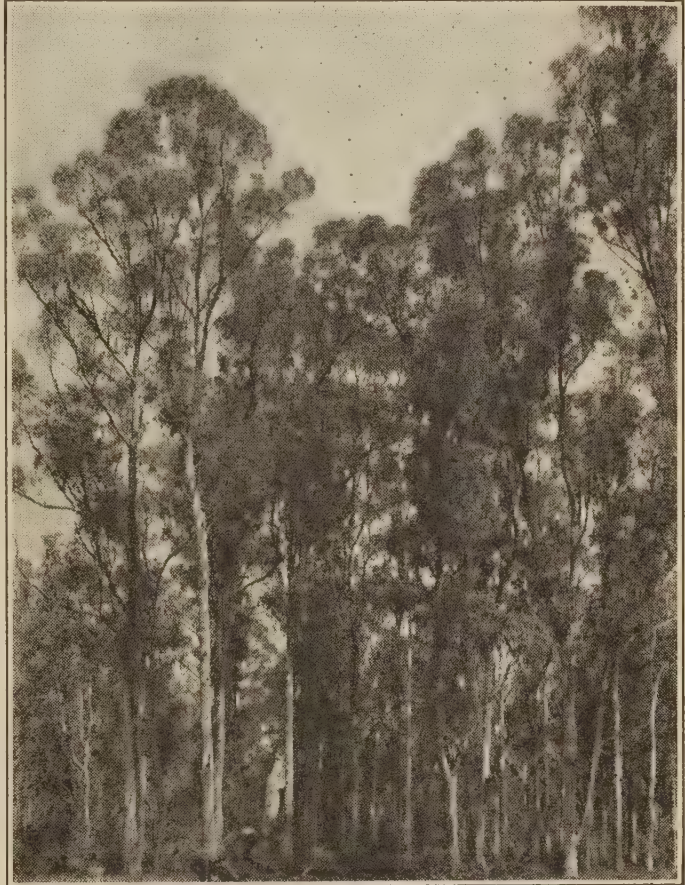


FIG. 241. Eucalyptus forest of Australia

species or groups of related species are often confined to one area or to a limited number of separate areas, and it is these species that give us the greatest information concerning the origin of plants and animals.

From geological evidence we find that all the continents have had land connections in the past, and, moreover, that many land areas which at present are islands were formerly connected with continents or with other islands. The floras of different regions and islands frequently differ widely from each other, and in general this difference increases with the length of time during

which the two areas have been separated from each other by barriers such as high mountains or seas. This is easily explained by the teachings of evolution. When there is communication between two contiguous areas, the plants and animals of the two areas are naturally interchanged. If later the two areas become separated, as by the submergence of land connections, the flora and fauna of each will continue their evolution separately. Owing to the method by which evolution takes place it is not to be expected that the course of evolution will be the same in the two different localities, but rather that evolution will take place in a different direction in each. In this way the longer the two areas are separated the more distinctly different their faunas and floras become. Australia has been separated from the rest of the land areas of the world for long ages, and as a result its fauna and flora are strikingly different from those of the rest of the world. The great development of eucalypts (Fig. 241) and marsupials in Australia is well known.

**Geological evidence.** This evidence is afforded by fossils. A *fossil* may be defined as any impression, remains, or trace of a plant or animal of a past geological age. By the study of fossils we learn much about the floras and faunas of past ages.

**Nature of fossils.** The most important types are *impressions* and *petrified structures*. We are all familiar with the impressions made by leaves in mud. Plants and animals are frequently buried and leave impressions. If these impressions remain after the material in which they are made is turned to rock, the result is a fossil. From such impressions (Figs. 242, 243) we can learn much concerning the form and shape of organisms or organs, but usually nothing of their internal structure. Among the most instructive fossils are those produced by petrification. In such cases the plant or animal material is replaced by stone, and it is frequently possible to study much of the microscopic structures of these fossils. In addition to the above classes of fossils we sometimes find the original material of organisms preserved.

**Formation of fossils.** The rocks of the earth's surface are divided into two classes, according to their origin: igneous and



sedimentary. *Igneous* rocks are produced as the result of heat and do not contain fossils. *Sedimentary* rocks are formed by the transportation of small rock particles and their subsequent deposition in another place; or they are the result of precipitation from solution, or of secretion by organisms, as in the case of limestones. Sedimentary rocks are the ones that yield fossils.

It is a common observation that most dead plants and animals are quickly destroyed by decay. They are not likely to be fossilized unless they are rather quickly covered by some protecting material. Also, oxygen must be largely excluded, as decay is dependent on oxidation. Such conditions are most usual in lakes, seas, or marshes. Organisms with hard parts are much more likely to be fossilized than are those without them. For this reason the very primitive and soft plants and animals are rarely fossilized.



FIG. 242. Fossil leaves

**Age of fossils.** In the formation of sedimentary rocks the oldest naturally occur at the bottom of the series and the youngest at the top. The most ancient fossils will be found in the oldest rocks, while the most recent fossils will be in the youngest rocks. In the past history of the earth, areas that were under the sea have risen and become dry land (Fig. 244), while some of the areas that were formerly dry land are now under the sea. Owing to erosion and the washing of materials from the land into the sea (Fig. 245) there is a general tendency for the surface of the dry land to be washed away, while that under the sea is built up by the

accumulation of deposited material. In this way rocks are built up while the land is submerged, and are worn away when the land is exposed.

Sometimes the same land has been elevated above the sea more than once. While the land is submerged, layers of rock are formed. When the land is exposed as the result of eleva-

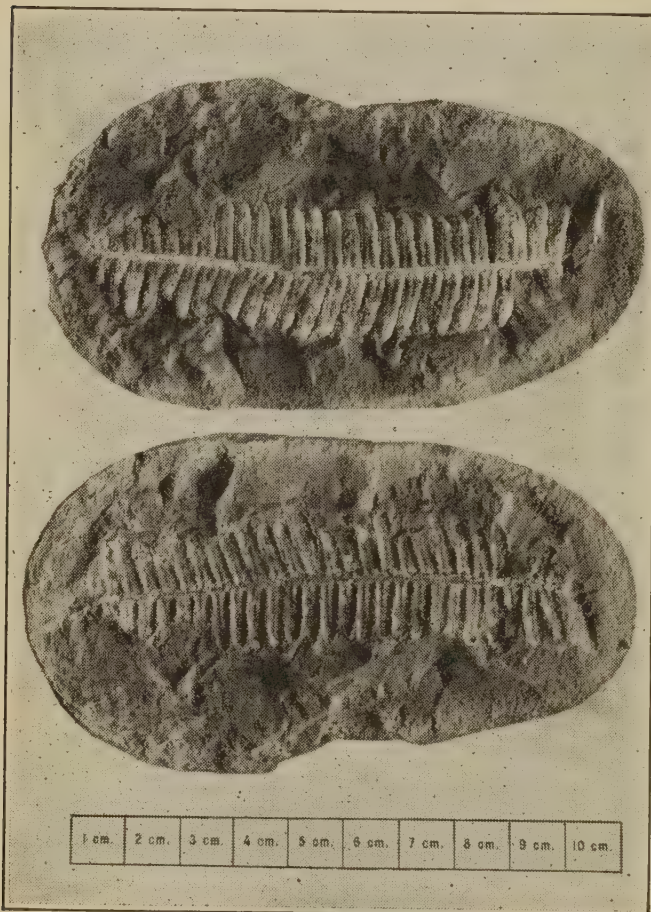


FIG. 243. Fossil leaf

tion, the rock begins to be eroded, and if the area is exposed for a long period, may be removed to a considerable depth. If such an area is again submerged, its surface will be covered by new layers of rock. There will be a great difference in age between the lowest of these new layers and the old layer on which it is deposited. This is due to the fact that during the time when the area was exposed no new layers were formed, and, moreover, much of the former rock was removed. Owing to such occurrences as

that just outlined, large gaps frequently occur in the geological records in a given series of rocks. By piecing together the geological records from various parts of the earth, however, it is possible to get much information concerning the relative ages of different rock strata.

**Incompleteness of fossil records.** While fossils have been formed in various ways, the great majority of them originated under water, and the discovery of most of them has been due to the emergence of land that was formerly submerged. When such fossils



are discovered it is usually owing to a combination of favorable circumstances. Fossils that are formed in deep seas are rarely seen, as such areas are not often elevated sufficiently to become dry land. When areas of fossil-bearing rocks are exposed to erosion, the fossils are uncovered, and in this way many fossils are brought to the attention of man; but those that were exposed in this manner in past ages have been destroyed, and in this way a great

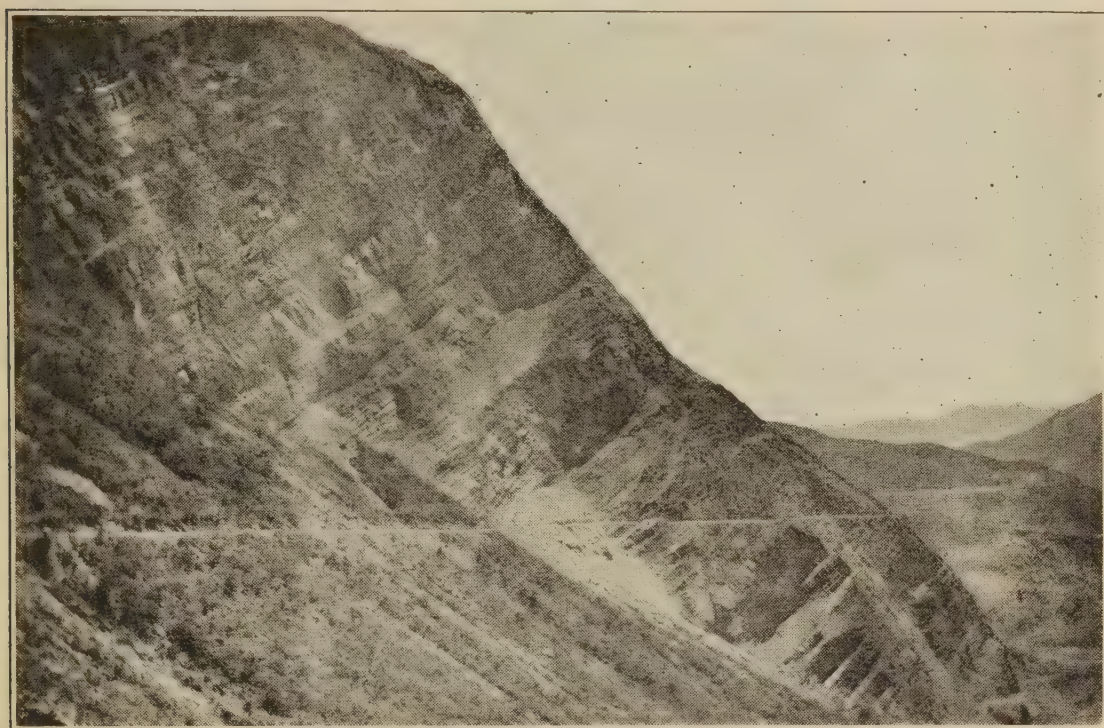


FIG. 244. Cliff more than a thousand feet high composed of alternately bedded sandstone and shales (Mountain Province, Philippine Islands)

deal of the fossil record has been lost. Fossils have also been destroyed by being dissolved from rocks, by being subjected to great pressure, and by various other means. As previously mentioned, the soft parts of organisms are rarely fossilized. Owing to the above-mentioned facts, and for other reasons, the fossil record is not as complete as we should like to have it, and, moreover, the study of such fossils as can be found is very far from complete; yet, in spite of its imperfections, the fossil record has given us considerable knowledge of the past history of floras and faunas.



**History as told by fossils.** The oldest plant fossils were all water plants with a simple organization, and belonged to that great composite group known as thallophytes. Thallophytes are not differentiated into stems and leaves. Flowering plants are relatively recent arrivals upon the scene. Between the age of thallophytes and the recent age of flowering plants there was



FIG. 245. Erosion on a mountainside (Taal Volcano, Philippine Islands)

a succession of many floras, the dominant elements of which showed an ever-increasing complexity. In the Carboniferous Age the forests contained trees that were a hundred or more feet in height, lacked both flowers and seeds, and reproduced by means of single cells called spores. No such trees have existed for many ages. In the Carboniferous Age there were also fernlike plants with seeds; these likewise died out ages ago. In general the dominant groups of the ancient land floras have either disappeared or are unimportant constituents of our present flora.

The fossil record shows that in animals also there has been a development from the simple to the complex, and that mammals



appeared late in geological history. The successive ages are frequently called the Age of Invertebrates, the Age of Fishes, the Age of Amphibians, the Age of Reptiles, and the Age of Mammals. These great groups of animals appeared in the above order and were dominant in the ages which bear their names. Animals of the early ages, such as gigantic amphibians and reptiles and the birdlike reptiles, have disappeared, and many of them have left no descendants or close relatives.

Incomplete as a fossil record is, it leaves no doubt that the plants and animals of one age were derived from those of a previous age by gradual changes, and that the accumulation of these changes through the long periods of geological time has resulted in an evolution from very simple ancestors to complex organisms.

**Course of evolution.** From what has been said about the causes of evolution it will be evident that evolution does not follow a straight line but that it rather pursues a branching course. A diagrammatic representation of the course of evolution is therefore drawn as we should draw the branches of a tree, rather than as a straight line. Because one form has given rise to a second form it does not follow that the first form will continue or ever again give rise to the second form. The evidence from geographical distribution supports the idea that the evolution of a given form will produce different results in different times and places, as, when two regions with similar floras and faunas become separated, their floras and faunas develop along different lines and the differences increase with the length of time the two areas are separated. We sometimes hear the question, If lower forms gave rise to certain higher forms in the past, why do they not continue to do so? In the first place, the ancestors of the higher forms are, for the most part, dead. In the second place, the evolution from one form to a very different form requires the combination of a great many circumstances acting through a long period of time, and it is not to be expected that all these conditions will ever exist more than once.

In view of the above, what is the relation between the simpler and the more complex plants that exist today? This question

can be answered by a hypothetical example. We will start with a very ancient and simple plant which we will call *A*. We will suppose that this plant gave rise to two different forms, *B* and *C*, which were naturally very much like their parent *A*. *B* and *C* were better fitted to their environment than *A*, and in the course of time *A* died out and disappeared, while *B* and *C* both survived. *B* was very thoroughly adapted to its environment, and it continued to exist through long ages and is a component of our present flora. *C* was either less fitted for its environment or for some other reason underwent further evolution and gave rise to form *D*, which in turn produced *E*, etc. As a descendant of *E* we have a living form, *X*, which is very different indeed from the parent form *A* and very much more complex. Now the relationship between *X* and *B* is clear. *X* is not a descendant of *B*, and *B* is very clearly not a descendant of *X*. *X* is, however, a descendant of *A*, which was very similar to *B*, so that we can say that, while *X* is not a descendant of *B*, it is a descendant of a form very similar to *B*. It seems very improbable that there still exist many, if any, of the forms of plants which were the direct ancestors of modern flowering plants, but it appears certain that many living forms are very similar to certain ancestral stages.

It does not follow that because a plant has a simple structure it is at a disadvantage as compared with more complex plants. Just as many trees are fitted for growing in the open, so many mosses are fitted for growing on trees, and many one-celled plants for floating in water.

**Evolution and modern thought.** The doctrine of organic evolution has come to be universally accepted by scientists, and it is not too much to say that it is the corner stone of modern biological science. The entire classification of plants and animals is based on the doctrine of evolution, while structures, functions, and activities are explained in the light of evolution.

In the past there has been considerable misunderstanding of the teaching of evolution, and consequently prejudice against it. Theories of evolution date back to the ancient Greeks, but the general acceptance of the idea of organic evolution is due to



the writings of Charles Darwin. After the appearance of his books many people asserted that evolution denied the existence of a supreme being. Darwin made no such statement, and it is now generally conceded that the doctrine of evolution is not opposed to the idea of the existence of a deity. Evolution is simply the orderly operation of natural law, and to say that the orderly operation of the law of evolution denies the existence of a supreme intelligence would be equal to saying that because the flow of rivers, the rise and fall of tides, and the movement of planets all obey the law of gravity, there can be no deity. If the law of gravity and the law of evolution do not affirm the existence of a supreme being, they at least do not deny it. It has been argued that the orderly operation of natural law is one of the greatest arguments for the existence of a supreme directing intelligence, and this argument applies equally well to gravitation and to evolution. Certainly the most purposeful and intelligent human beings are those whose actions are orderly and predictable, while we have insane asylums for those whose thoughts and actions are lacking in order.

The statement has been frequently made that, according to the doctrine of evolution, man is descended from the monkey. Such a statement is not in accord with, but is opposed to, the teachings of evolutionists. What evolution does teach is that both man and monkey had a common ancestor, and not that one was derived from the other. The idea that man is descended from lower forms of life, instead of being a discreditable and discouraging belief, is really one that is full of encouragement. We have ascended a long way, but we may have hopes of improving the race still further if we but use our increasing knowledge of inheritance and evolution.

## CHAPTER IX

### THE FRUIT AND THE SEED

#### THE FRUIT

The term *fruit*, in the botanical sense, is used to denote that part of the plant in which the seeds are found. It consists essentially of the ripe ovary, but it may also include other floral parts which are connected with the ovary. The name *fruit*, used in this sense, includes much more than the popular term *fruit*;



FIG. 246. Collective fruit of mulberry

Left, a female flower ( $\times 3$ ); center, entire fruit ( $\times 1\frac{1}{2}$ ); right, single mature fruit in which the fleshy portion consists of enlarged calyx ( $\times 3$ )

it embraces not only what are generally known as fruits but also some vegetables, and even dry, inedible structures. To the botanist cucumbers, tomatoes, or bean pods with the included seeds are just as truly fruits as are apples and oranges.

**Collective and aggregate fruits.** Most fruits are structures derived from one ovary in one flower. In some cases a number of separate flowers may form a *collective* fruit (Figs. 246, 247, 256) as in the pineapple. In other cases an *aggregate* fruit may be formed from several ovaries produced in one flower (Figs. 248, 249).



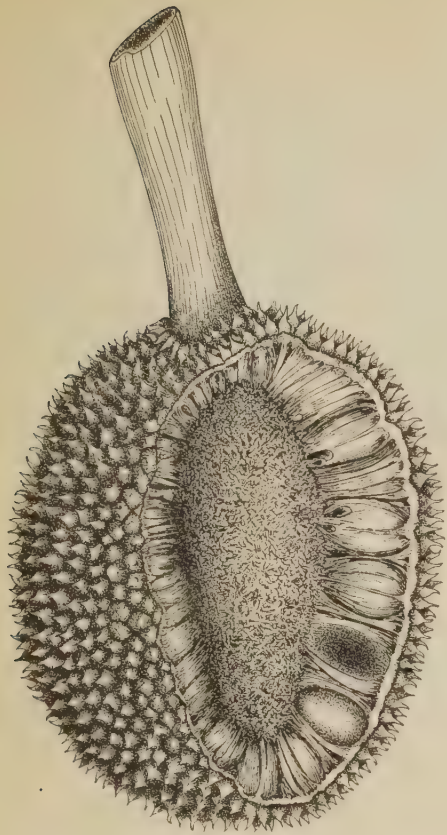


FIG. 247. Collective fruit of breadfruit (*Artocarpus communis*). ( $\times \frac{1}{3}$ )



FIG. 248. Aggregate fruit of strawberry  
The fleshy portion is an enlarged torus. ( $\times 1$ )

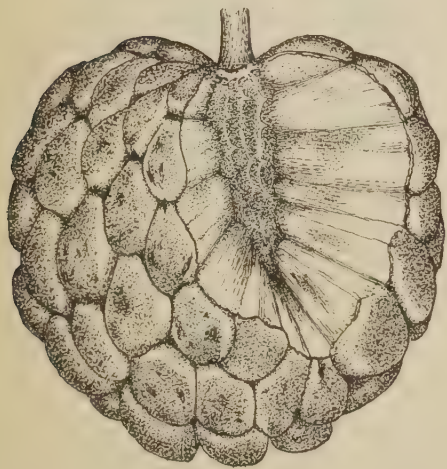


FIG. 249. Aggregate fruit of sugar apple (*Anona squamosa*). ( $\times \frac{1}{2}$ )

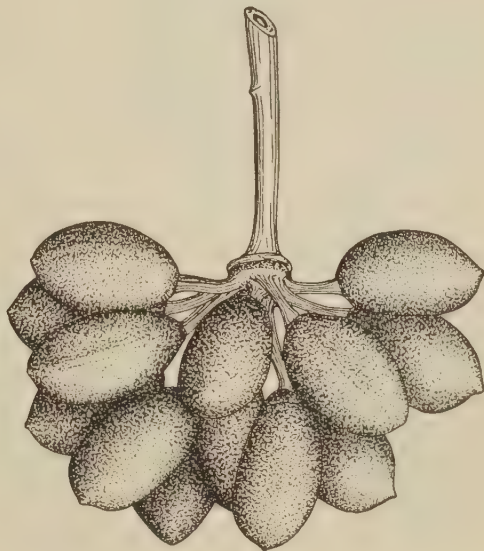


FIG. 250. Separate fruits of ylang-ylang (*Canarium odoratum*) formed from separate ovaries in the same flower. ( $\times \frac{2}{3}$ )

**Composition of fruits.** Some fruits are produced by superior ovaries, and others by inferior ones. An ovary is said to be *superior*

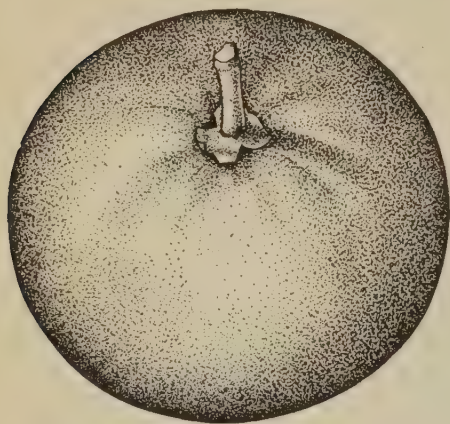


FIG. 251. Grapefruit developed from superior ovary

Note remains of calyx at base of fruit. ( $\times \frac{2}{5}$ )

when the point of attachment of the calyx and corolla is below the ovary (Figs. 202, 203), and *inferior* when the point of attachment is above the ovary (Figs. 208, 221). In the latter case the torus may be considered as having a bottle-like form, at the summit of which the calyx, corolla, and stamens are attached. In such cases the torus takes part in the formation of the fruit. When the fruit is derived from a superior ovary, the remains of the calyx can frequently be found at the

base of the fruit, as in the grapefruit (Fig. 251). When the ovary is inferior, the remains of the calyx can sometimes be plainly seen

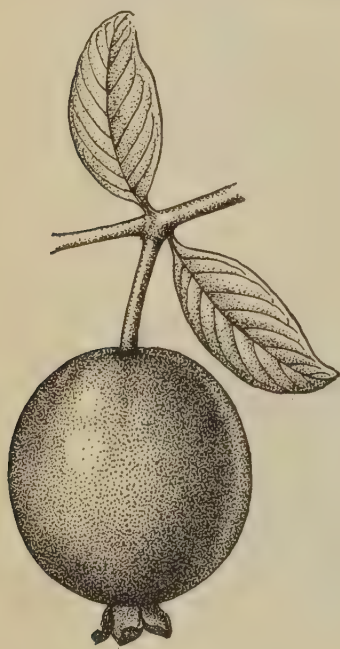


FIG. 252. Berry of guava developed from an inferior ovary. ( $\times \frac{1}{4}$ )

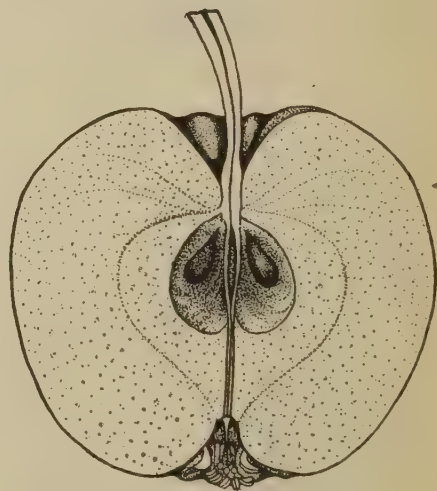
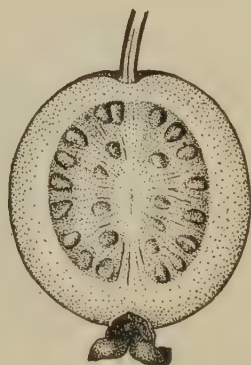


FIG. 253. Cross section of an apple fruit, showing ripened ovary surrounded by enlarged torus. ( $\times \frac{1}{2}$ )

at the apex of the fruit (Fig. 252). In the flower of the apple there are five imperfectly fused carpels which are more or less





FIG. 254. Cashew fruit

The large fleshy part is the thickened torus.  
( $\times \frac{1}{2}$ )

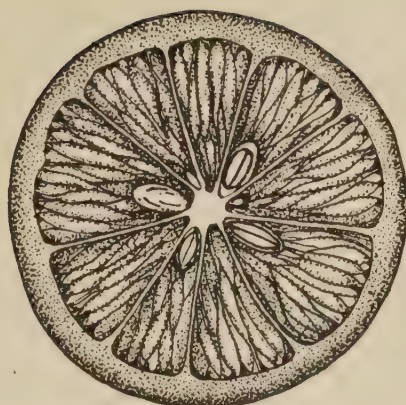


FIG. 255. Cross section of fruit of lime

The fleshy part consists of hairs from ovary walls.  
( $\times 1$ )



FIG. 256. Collective fruit of fig

These separate fruits are surrounded by an enlarged stem. ( $\times 1$ )



FIG. 257. Various forms of capsules

Left, *Illicium verum* ( $\times \frac{1}{2}$ ); second figure, *Argemone mexicana* ( $\times \frac{1}{2}$ ); third figure, *Abutilon indicum* ( $\times \frac{1}{2}$ ); fourth figure, *Abelmoschus moschatus* ( $\times \frac{1}{2}$ ); upper right, *Celosia argentea* ( $\times 4$ ); lower right, *Bixa orellana* ( $\times \frac{1}{2}$ )

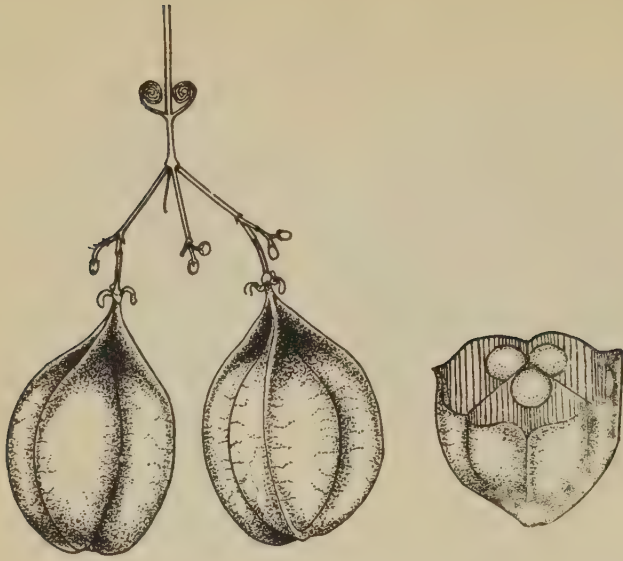


FIG. 258. Inflated capsule of *Cardiospermum halicacabum*. ( $\times \frac{2}{3}$ )

tion is formed by hairlike outgrowths from the walls of the ovary (Fig. 255). The fleshy part in some cases is composed

inclosed in a cuplike torus. During the formation of the fruit the carpels fuse with the torus and form the apple fruit. In this (Fig. 253) the ovary is represented by the core and the torus by the surrounding fleshy portion.

In some fleshy fruits the fleshy part consists entirely of the enlarged torus (Figs. 248, 254). In

the lime the fleshy portion

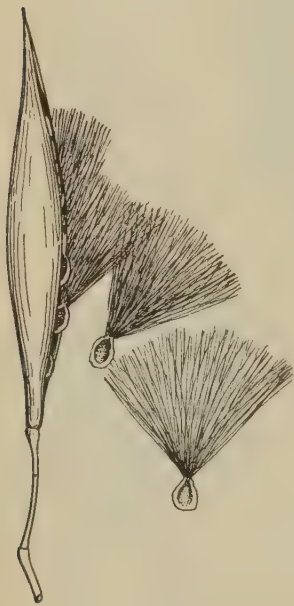


FIG. 259. Follicle of a milkweed (*Asclepias curassavica*), showing liberation of seed with hairy appendages. ( $\times \frac{1}{2}$ )

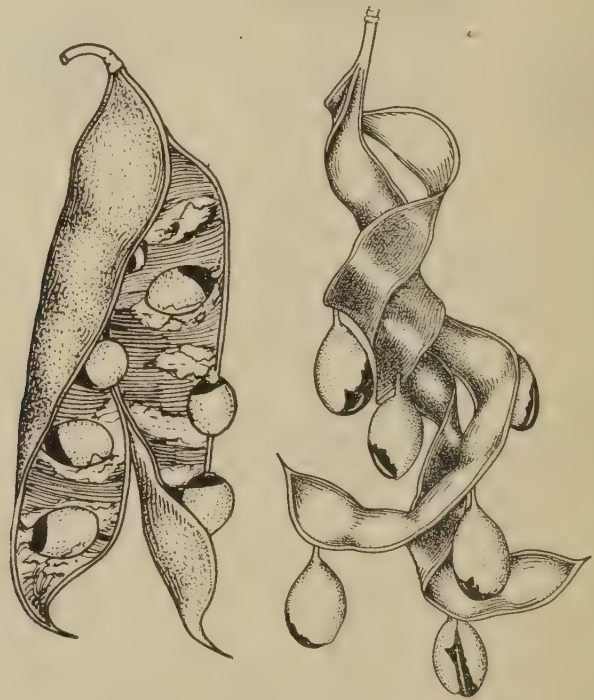


FIG. 260. Unusual types of pods

Left, *Abrus precatorius* ( $\times 1$ ); the seeds are very hard and bright red, with black spots at one end, and, although indigestible, are dispersed by birds. Right, *Pithecolobium dulce* ( $\times \frac{1}{2}$ ); the seeds have a white fleshy covering and are dispersed by birds





FIG. 261. Achenes of *Elephantopus*, *Cosmos*, and *Bidens* (beggar-ticks)

These are dispersed by adhering to animals. ( $\times 2\frac{1}{5}$ )

*fleshy*. The dry fruits may be subdivided into *dehiscent* fruits, or *capsules*, and *indehiscent* fruits. Dehiscent fruits are those

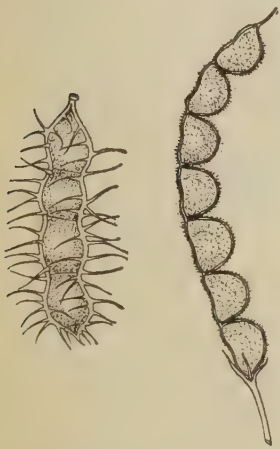


FIG. 263. Schizocarpic pods of sensitive plant (*Mimosa pudica*) and tick trefoil (*Desmodium gangeticum*). ( $\times 1$ )

of the outer coverings of the seeds (Fig. 285). In the mulberry (Fig. 246) the fleshy part consists largely of thickened, fleshy calyx lobes. The collective fruit of the pineapple is composed of a central axis and numerous flowers which become fleshy. The fig is a hollow, pear-shaped inflorescence on the inside of which are many flowers (Fig. 256). These flowers are developed into many small, seed-like fruits which are frequently mistaken for seeds.

**Classification of fruits.** Fruits are usually divided into two classes, *dry* and

which open at maturity so that their seeds can escape, while indehiscent ones are those

which do not open. Indehiscent fruits may be further subdivided into *achenial* and *schizocarpic* fruits. The fleshy fruits may be divided into *drupes* and *berries*.

**Capsules.** Dry, several-seeded to many-seeded dehiscent fruits are known as capsules. Capsules are of many shapes, and they open in many different ways (Figs. 257, 271, 279, 280). The *legume*, or *pod*, and the *follicle* are special kinds of capsules. The follicle and the legume are each derived from an



FIG. 262. Samaras of *Securidaca corymbosa* and *Tarrietia sylvatica*. ( $\times \frac{2}{5}$ )

ovary composed of a single carpel. The follicle splits along one side only (Fig. 259), while the legume, which is the characteristic fruit of the pea or bean family, usually splits along two edges (Fig. 260).

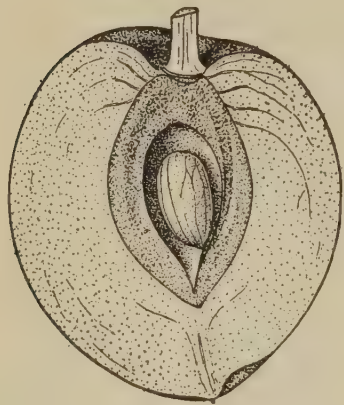


FIG. 264. Longitudinal section of drupe of peach. ( $\times \frac{1}{2}$ )

is a winged achene (Fig. 262). The *nut* is a one-seeded, usually indehiscent fruit in which the wall of the fruit, or the pericarp, is hard. Many structures which are popularly called nuts do not fit this description.

**Schizocarpic fruits.** These are dry fruits which split up into a number of one-seeded, usually indehiscent parts (Fig. 263), as in the castor-oil plant.

**Drupes.** A drupe is a fruit in which the inner part of the *pericarp* (ripened ovary wall) is hard and the outer part fleshy or fibrous (Figs. 264, 265, 304). In the pericarp of the drupe there are three regions: the epicarp, or outer skin; the mesocarp, or middle fleshy or fibrous region; and the endocarp, or hard inner portion which forms the stone inclosing the seed. Many structures popularly known as nuts are composed of the endocarps and the seeds of drupes. The walnut and the almond are examples.

**Achenial fruits.** An *achene* is a small, dry, indehiscent, one-seeded fruit (Fig. 261). The achenes of the sunflower are sold under the name of *sunflower seed*. The *caryopsis*, or *grain*, differs from the achene in that the pericarp, or wall, of the fruit, is fused with the testa (the outer covering of the seed). The *grain* is the typical fruit of the grasses, and its structure can be observed very clearly in corn (Fig. 303). The *samara*

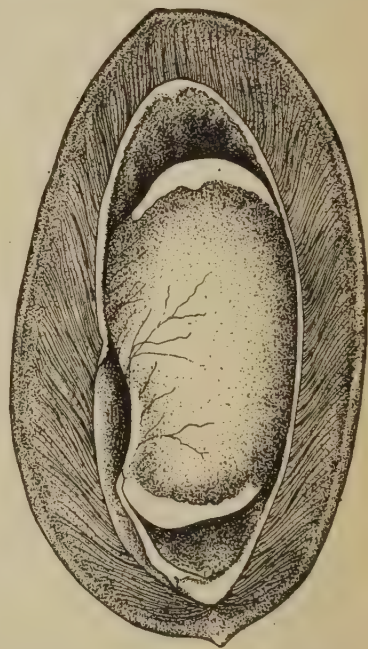


FIG. 265. Longitudinal section of drupe of mango (*Mangifera indica*). ( $\times \frac{1}{2}$ )



**Berries.** Fleshy, indehiscent, few-seeded to many-seeded fruits are known as berries (Figs. 266, 267). The word *berry*, like the word *fruit* or the word *nut*, has thus very different botanical and popular meanings. The date is a one-seeded berry, as the "stone" is the seed and not the endocarp. Tomatoes, grapes,



FIG. 266. Berry of sapodilla or chico  
(*Achras sapota*). ( $\times \frac{1}{2}$ )

FIG. 267. Cross section of berry  
of cucumber. ( $\times \frac{1}{2}$ )

and bananas are berries, while oranges, cucumbers (Fig. 267), melons, and apples are examples of special classes of berries.

**Classification inexact.** In discussing the different types of fruits it is convenient to use some such classification as that given above, although it should be realized that any classification must be arbitrary and in many cases inexact. The fruit of the balsam (Fig. 288) is a somewhat fleshy capsule. Many capsules have no regular method of dehiscence.

## THE SEED

A *seed* is a structure developed from an ovule. It consists of an embryo, stored food which may be either in or around the embryo, and one or two coverings called *seed coats* (Figs. 268, 269).

**The embryo.** This consists of a small undeveloped shoot called the *plumule*, a cylindric structure known as the *radicle*, which will develop into a root, and one or two large leaves which are the *cotyledons*, or seed leaves (Figs. 268, 270). Plants with one cotyledon (Figs. 303, 304) are called *monocotyledons*, while those with two (Fig. 268) are called *dicotyledons*.

**Endosperm.** In some seeds, such as the squash seed and the lima bean, the cotyledons are large and fleshy and are filled with stored food (Figs. 268, 270). In others the cotyledons are thin and are surrounded by a mass of food-storage tissue, the *endosperm*, as in the seed of the castor-oil plant shown in Fig. 269. Most seeds of flowering plants contain an endosperm at some stage of their development, and the food stored in this endosperm is absorbed by the cotyledons. In

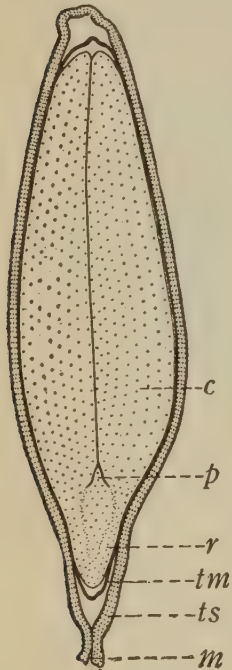


FIG. 268. Longitudinal section of squash seed

*c*, cotyledon; *p*, plumule; *r*, radicle; *tm*, tegument; *ts*, testa; *m*, micropyle. ( $\times 3$ )

The endosperm has its origin at the time of fertilization. After the pollen tube has grown down into the ovule it discharges two male nuclei into the embryo sac. One of these unites with the nucleus of the egg, and the fertilized egg develops and becomes the embryo. The other male nucleus unites with the two polar nuclei. This fusion nucleus undergoes divisions resulting in the production of the endosperm tissue in the embryo sac around the embryo.

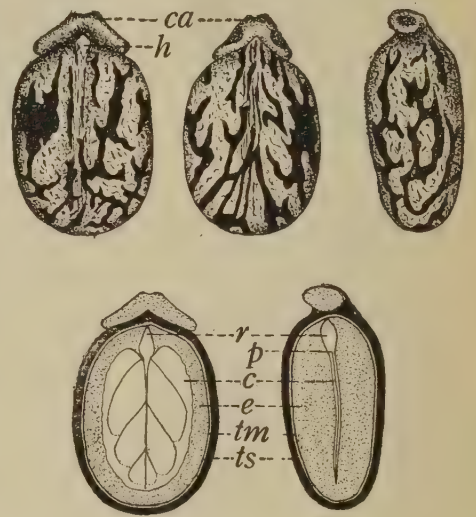


FIG. 269. Ventral, dorsal, and lateral views of seed of castor-oil plant (*Ricinus communis*), with section of seed

Above: *ca*, caruncle; *h*, hilum. Below: at left, section cut from side to side; at right, section cut perpendicular to dorsal surface; *r*, radicle; *p*, plumule; *c*, cotyledon; *e*, endosperm; *tm*, tegument; *ts*, testa. ( $\times 2$ )



**Perisperm.** In the ovule the embryo sac is surrounded by the nucellus. Just as the embryo absorbs food material from the endosperm, so the endosperm absorbs food material from the nucellus. In most seeds the nucellus is entirely absorbed before the seed is ripe, and even the inner integument may be so absorbed. In some cases, however, the ripe seed contains an embryo surrounded by the endosperm, and this, in turn, by the nucellus. When the nucellus remains in the mature seed it is known as perisperm.

**Seed coats.** The seed coats are derived from the integuments of the ovule. The outer seed coat, or *testa*, develops from the

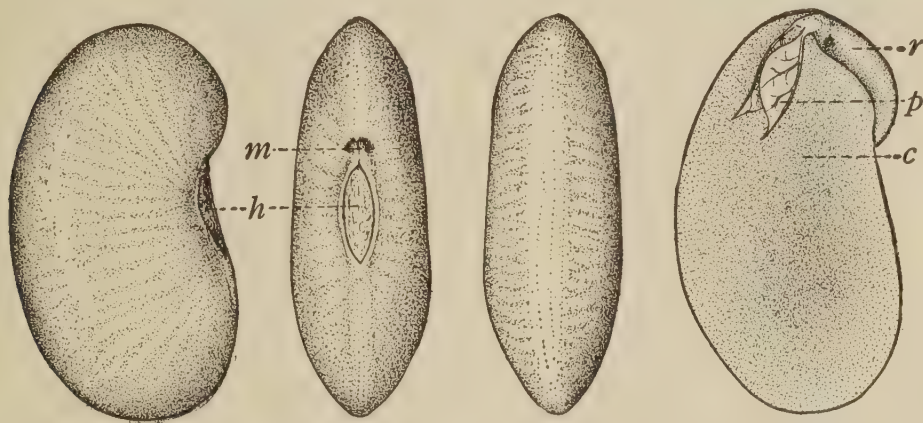


FIG. 270. Lima bean, showing ventral, dorsal, and lateral views and embryo. At left: *m*, micropyle; *h*, hilum. At right: embryo with seed coat and one cotyledon removed; *r*, radicle; *p*, plumule; *c*, cotyledon. ( $\times 1\frac{1}{2}$ )

outer integument. The testa is usually thick and hard (Fig. 268). The inner seed coat, or *tegmen*, is usually thin (Fig. 268). This is derived from the inner integument. In some cases there is only one seed coat.

**Hilum.** On the testa there is a scar marking the place where the funiculus was attached to the ovule (Fig. 270). This scar is known as the hilum.

**Micropyle.** The testa is pierced by a small hole, the micropyle (Fig. 270), which is the same structure as the micropyle in the ovule. The tip of the radicle points toward the micropyle.

## SEED DISPERSAL

We have seen that the seed consists of an embryo, stored food material, and a protective covering. The embryo is ca-

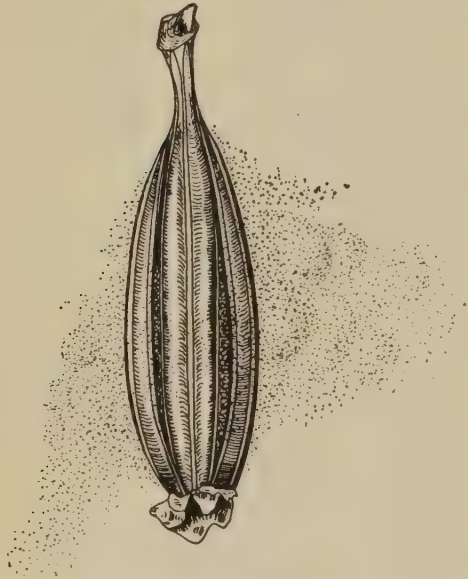


FIG. 271. Capsule of an orchid (*Cymbidium finlaysonianum*) open and with minute seeds being scattered by the wind. ( $\times \frac{1}{2}$ )

pable of growing into a plant, and the stored food material furnishes it with a supply of food for its growth in the period before it has become established. Most seeds are also provided with some means of dispersal. Without this the great majority of seeds would fall under the parent plant and not be carried to a location favorable to germination and growth. The mechanism of dissemination may be a part of the seed itself or may belong to surrounding portions of the fruit. The principal agencies by which seeds are dispersed are wind, water, animals, and explosive mechanisms.

**Dispersal by wind.** Either the whole fruit or the individual seeds may be suited to dispersal by wind. Seeds that are thus disseminated are characteristically light. The means of adaptation to wind dispersal may be grouped under the headings of *minute seeds*, *feathery appendages*, *flattened fruits or seeds*, *winglike outgrowths*, and the so-called *censer mechanisms*.

**Minute seeds.** The seeds of orchids are very small and, besides, have a light, inflated outer covering. These dust-like seeds can be blown by the wind for great distances (Fig. 271).

**Wings.** In many cases seeds, and in others whole fruits, are flattened or have winglike outgrowths (Figs. 272, 273), or they

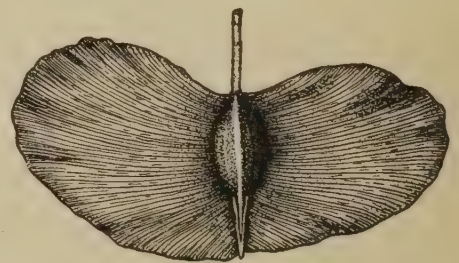


FIG. 272. Flattened wing fruit of *Terminalia calamansanay*. ( $\times \frac{1}{2}$ )





FIG. 273. Flattened fruits of ash, adapted to wind dispersal. ( $\times 1\frac{1}{6}$ )



FIG. 275. Follicles of *Pterocymbium tinctorium*, adapted to wind dispersal. ( $\times \frac{1}{2}$ )



FIG. 274. Flattened seed of *Macrozania* with large, papery wing. ( $\times \frac{5}{12}$ )



FIG. 276. Fruit of *Dipterocarpus grandiflorus*, with wings formed by enlarged calyx lobes. ( $\times \frac{1}{3}$ )



FIG. 277. Fruit of linden, adapted to wind dispersal by being attached to a specialized leaf (bract).

( $\times \frac{2}{3}$ )

the capsules are violently shaken, as by a strong wind (Figs. 257, 279, 280). This has a tendency to scatter the seeds. The seeds may in addition have a flat shape (Fig. 279) or winged outgrowths; and as they are most likely to escape when there is a strong wind, they may be blown for considerable distances.

**Dispersal by water.** Adaptations for dispersal by water are not so common as are those for dispersal by wind, but the former occur in many seashore and aquatic

may be both flattened and winged (Fig. 274). This type of structure results in the scattering of the seed by the wind.

**Feathery appendages.** Seeds (Fig. 259) or fruits (Fig. 278) may have feathery appendages which greatly increase their buoyancy, so that they are frequently carried by the wind to considerable altitudes. These feathery appendages are very characteristic of the seeds of milkweeds (Fig. 259) and of the achenes of many composites (Fig. 278). Commercial cotton consists of trichomes which grow from the epidermal cells of the seed of the cotton plant. These trichomes form a flossy mass around the seed.

**Censer mechanisms.** The capsules of many plants open in such a way that the seeds can escape only when

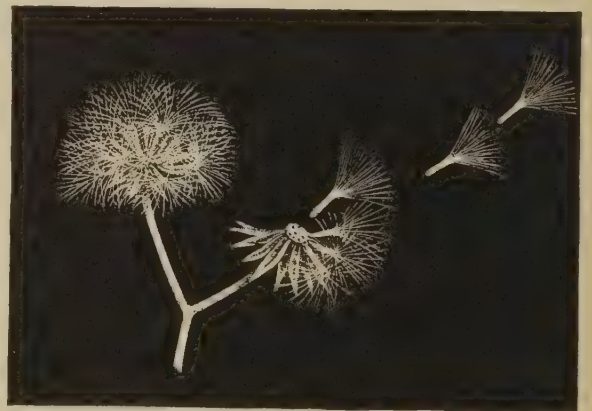


FIG. 278. Fruits (achenes) of ironweed (*Vernonia*), suited to dispersal by wind on account of their hairy appendages





FIG. 279. Capsule of *Aristolochia elegans*

It hangs in such a position that the seeds are liberated only when it is shaken by the wind. The flattened seeds are adapted to wind dispersal. ( $\times \frac{1}{2}$ )

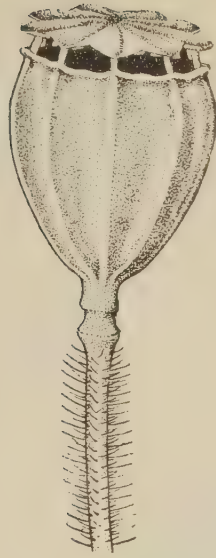


FIG. 280. Capsule of poppy

The seeds are liberated only when the capsule is shaken rather violently. ( $\times 2\frac{1}{2}$ )



FIG. 281. Fruit of *Terminalia catappa*, adapted to dissemination by water by having a thick, fibrous husk. ( $\times \frac{1}{2}$ )

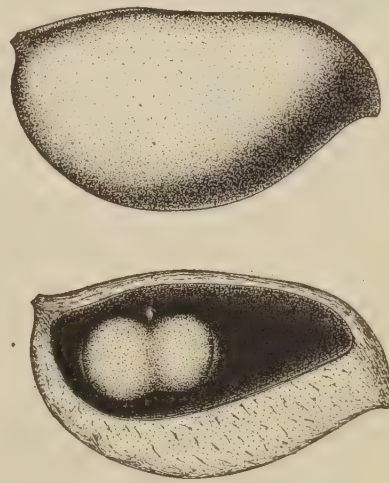


FIG. 282. Fruit of *Heritiera littoralis*, adapted to dissemination by water by having a thick, fibrous husk inclosing an air cavity. ( $\times \frac{1}{2}$ )

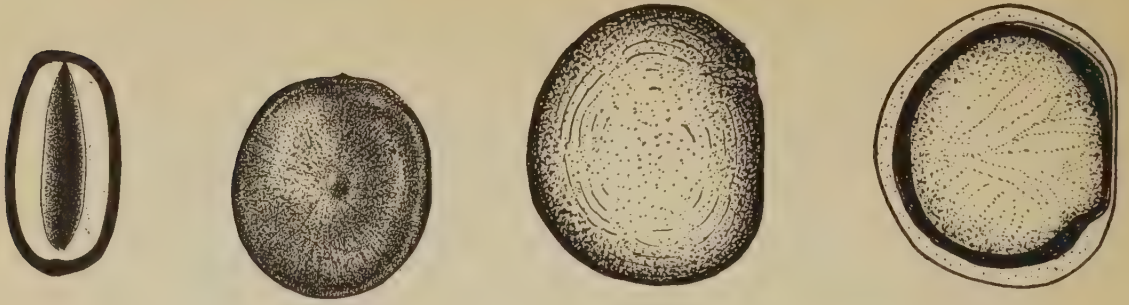


FIG. 283. Seeds of *Entada scandens* ( $\times \frac{1}{2}$ ) and *Mucuna gigantea* ( $\times 1$ )

These are adapted to dispersal by water by having an impervious seed coat and by containing an air cavity (in the first case between the cotyledons, and in the second around the embryo)



FIG. 284. Fruit of *Nelumbium nelumbo*

Below are the remains of the stamens. The large part above is the enlarged torus, the fruits being in depressions in the torus. The fruits float, and besides, the enlarged torus is replete with air cavities and is very buoyant. ( $\times \frac{1}{2}$ )

plants. Either the whole fruit or the seed may be adapted for floating. The pericarp of a fruit may be composed of light tissue (Fig. 281), or the fruit may be inflated (Fig. 282). The coconut (Fig. 304) is an excellent example of a fruit with a light pericarp. Floating seeds may likewise contain either a mass of light tissue or large air spaces (Fig. 283). In the lotus fruit (Fig. 284) the torus is a greatly enlarged mass of loose, air-filled tissue which floats readily, while the individual fruits are also adapted for floating. Many seeds that are not especially fitted for floating may occasionally float for short distances, or seeds that by themselves would not float may be carried in floating débris.

**Dispersal by animals.** Seeds that are adapted for dispersal by animals are disseminated in two general ways: in the case of fleshy fruits a portion of the fruit is eaten by the animal, while many dry fruits adhere to animals.

*Fleshy fruits.* Fleshy fruits are generally adapted to being eaten by animals. Such



fruits are usually constructed so that the fleshy part may be eaten without injury to the seed. In many cases the seed coat is very hard, while in drupes the seed is protected by the stony endocarp. Owing to this protection a seed may pass without injury



FIG. 285. Double follicle of *Tabernaemontana pandacaqui*

The follicle to the right has opened. The seeds are suited to dispersal by animals by having brilliantly colored, fleshy coverings. ( $\times \frac{1}{2}$ )

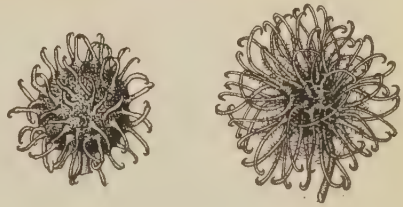


FIG. 286. Fruits adapted to dissemination by having hooks which adhere to animals

Left, *Triumfetta bartramia* ( $\times 2$ ); right, *Triumfetta annua*. ( $\times 1$ )

through the digestive tract of an animal. Birds are particularly prominent in disseminating the seeds of fleshy fruits. Sometimes they eat the fleshy portion of a fruit and throw the seeds away.

*Adhesive fruits.* Many dry fruits have hooklike appendages (Figs. 261, 263, 286) which are particularly fitted for grasping



FIG. 287. Seed of *Hyptis suaveolens*, adapted to dissemination by animals by having a mucilaginous covering which swells and is very sticky when wet

Left, dry seed ; right, wet seed. ( $\times 4$ )

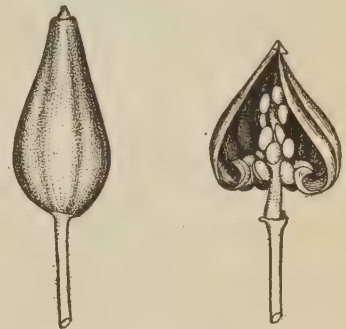


FIG. 288. Fruit of *Impatiens balsamina*, which explodes and scatters the seeds. ( $\times 1$ )

the hair of animals. Animals to which the fruits adhere carry them about and thus distribute the seeds. In a similar way fruits may adhere to clothing and thus be disseminated by man. Some seeds and fruits have a sticky covering which will adhere to the hair of an animal (Fig. 287).

*Minute seeds.* Many plants have minute seeds which are disseminated by being caught in mud that adheres to the feet or other parts of birds or other animals.

**Dispersal by explosive mechanisms.** Many fruits are so constructed that they explode when ripe and scatter the seeds. This method of dispersal is frequently conspicuous in members of the

bean family, where the explosive forces are due to stresses arising from the drying of the valves of the pod. The balsam has somewhat fleshy capsules which are very turgid. When these are disturbed by contact the segments of the pericarps roll up with considerable force and in such a way that they scatter the seeds (Fig. 288).

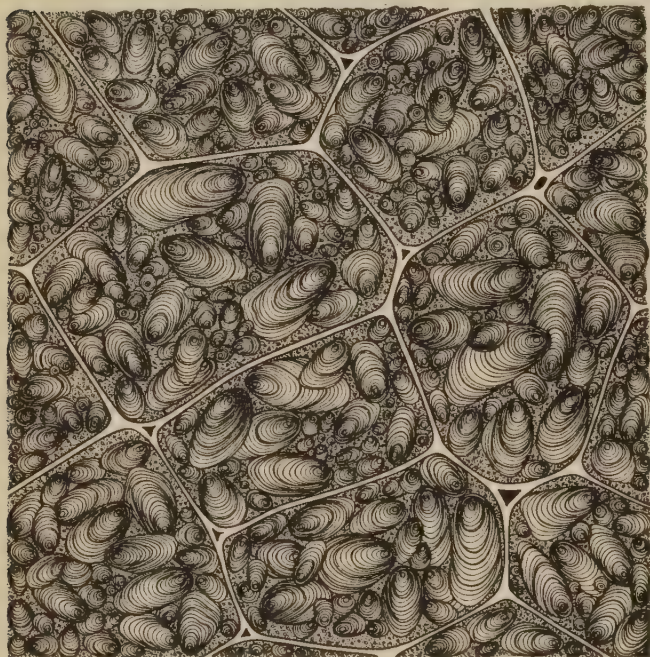


FIG. 289. Section showing a few cells of a potato tuber

The cells contain large and conspicuous grains of starch and a small amount of small granules of protein. ( $\times 156$ )

future use. Food may be stored in certain parts of ordinary stems and roots; in especially modified stems, as in the potato and ginger; in modified roots, as in sweet potatoes; or in modified leaves, as in the onion. Seeds almost always contain a large amount of stored food, which nourishes the young plants until they become established. Reserve foods are of three general classes: carbohydrates, fats and oils, and proteins.

**Carbohydrates.** Carbohydrates are organic compounds composed of carbon, hydrogen, and oxygen, the hydrogen and oxygen usually being in the same proportion as in water. In

## RESERVE FOOD

When a plant manufactures more food than it needs for immediate use, the surplus is stored for



general the natural carbohydrates contain six, or some multiple of six, carbon atoms. The simple carbohydrates have a sweet taste and are known as sugars.

The forms of carbohydrates in which food is stored most abundantly are sugars and starches. Other forms are hemicellulose, or reserve cellulose, and inulin.

*Sugars.* The three sugars that are found most abundantly in plants are *glucose* (grape sugar), *fructose* (fruit sugar), and *sucrose* (cane sugar). Glucose and fructose have the formula  $C_6H_{12}O_6$ . They are thus composed of the same kinds of atoms in the same proportion, but the arrangement in the molecule is different. The simplest natural sugars have this formula and are known as monosaccharides. Sucrose ( $C_{12}H_{22}O_{11}$ ) has twice as many carbon atoms and is a disaccharide. It may be regarded as composed of one molecule of glucose and one of fructose, which are linked together with the dropping out of one molecule of water. Sucrose is familiar as the ordinary granulated sugar of commerce, which is obtained from sugar cane or sugar beets. Maple sugar also is sucrose. Glucose and fructose are found in nearly all plants, and glucose is an ingredient of a thick sirup, which is made by treating starch with dilute sulphuric acid and afterward removing the acid. Such sirups are frequently called corn sirups, as cornstarch is most commonly used in their preparation.

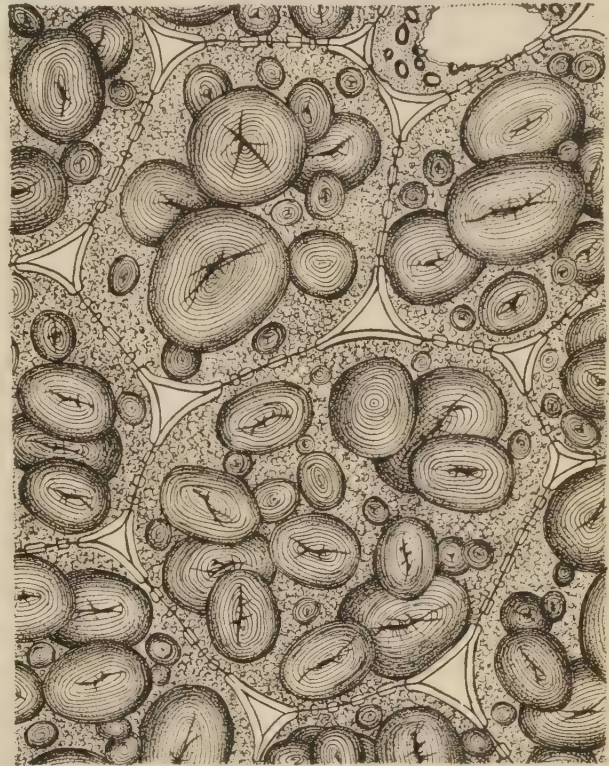


FIG. 290. Section of a few cells of mungo bean (*Phaseolus radiatus*)

The cells contain large and conspicuous grains of starch and small granules of protein. ( $\times 270$ )

*Starch.* Starch is a polysaccharide having the general formula  $(C_6H_{10}O_5)_n$ , in which  $n$  is a large number. Starch is insoluble

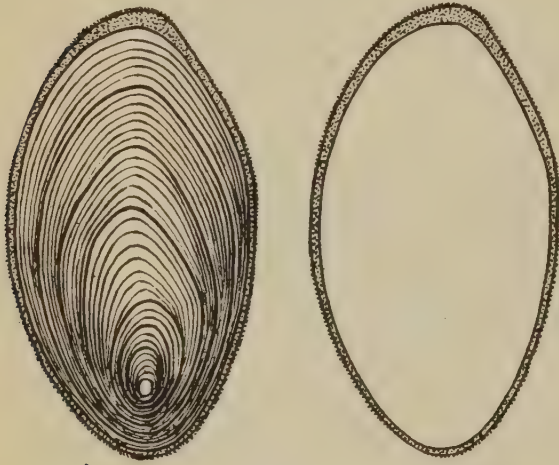


FIG. 291. Single grain of potato starch within an amyloplastid (left) and amyloplastid with starch grain removed (right). ( $\times 765$ )

in cold water and occurs in plants in the form of grains (Figs. 34, 289, 290). Starch grains from different plants have different shapes and configurations. Owing to this fact it is possible to identify starches by the use of a microscope. The starch grains are found in amyloplastids (Fig. 291). Starch is formed from sugar and is easily converted into sugar, either in plants or in a chemical laboratory. The storage of carbohydrates in

the form of starch has the advantage that the starch is insoluble and therefore does not produce excessive osmotic pressure.

*Inulin.* Inulin, like starch, is a polysaccharide and belongs to the general class of starches. In some plants, particularly the *Compositae*, inulin occurs in considerable quantities. Inulin is soluble in water and occurs in plants in solution. It can be precipitated by alcohol, when it forms characteristic spherocrystals (Fig. 292). After being extracted from plants it is a white powder like starch in appearance.

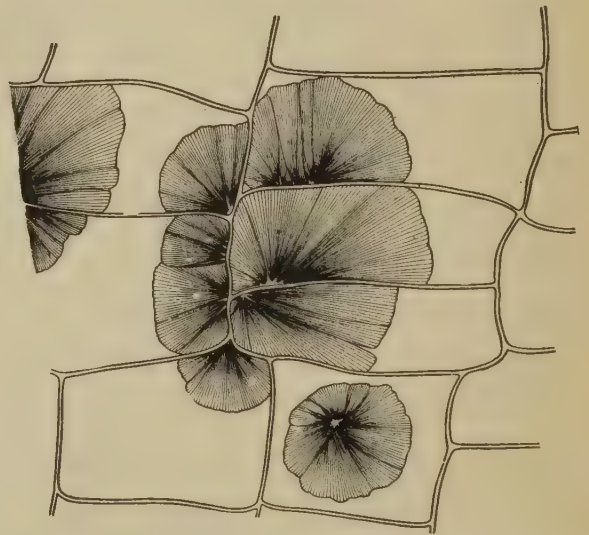


FIG. 292. Spherocrystals of inulin in cells of dahlia root. ( $\times 304$ )

*Hemicellulose.* In some seeds food is stored in thickened cell walls in the form of hemicellulose, or reserve cellulose. Food is stored in this form, however, much more rarely than as sugar



or starch. Reserve cellulose is found in some palm seeds and also in the seeds of some other plants (Figs. 14, 293, 294).

**Fats and oils.** The natural fats and fatty oils in plants and animals all belong to the same general class of compounds and are composed of glycerin ( $C_3H_5(OH)_3$ ) combined with organic acids. Glycerin has three OH groups which can be replaced by acid radicals. In natural fats all the groups are replaced, so that natural fats are triglycerides. Fats are composed of carbon, hydrogen, and oxygen, and are characterized by a small percentage of oxygen, as may be seen from the formulas of such common fats as stearin ( $C_{57}H_{110}O_6$ ), palmitin ( $C_{51}H_{98}O_6$ ), olein ( $C_{57}H_{104}O_6$ ), and linolein ( $C_{57}H_{98}O_6$ ). Owing to the very small percentage of oxygen contained in fats, the oxidation of fats produces large amounts of energy. More energy is obtained by oxidizing a given volume of fats than by oxidizing a similar volume of any known kind of compound that is found in either plants or animals.

Fats may be solid or liquid (oils), according to the temperature. Fatty oils occur in plants in the form of globules (Figs. 295-298).

**Proteins.** The proteins are the most important group of compounds found in plants, as they constitute the active matter of protoplasm, and the chemical phenomena of life processes are associated with them.

Proteins are exceedingly complex compounds, as will be seen from formulas which have been calculated for such representative proteins as zein ( $C_{736}H_{1161}N_{184}O_{208}S_3$ ), from Indian corn; gliadin ( $C_{685}H_{1063}N_{196}O_{211}S_5$ ), from wheat; casein ( $C_{708}H_{1130}N_{180}O_{224}S_4P_4$ ),

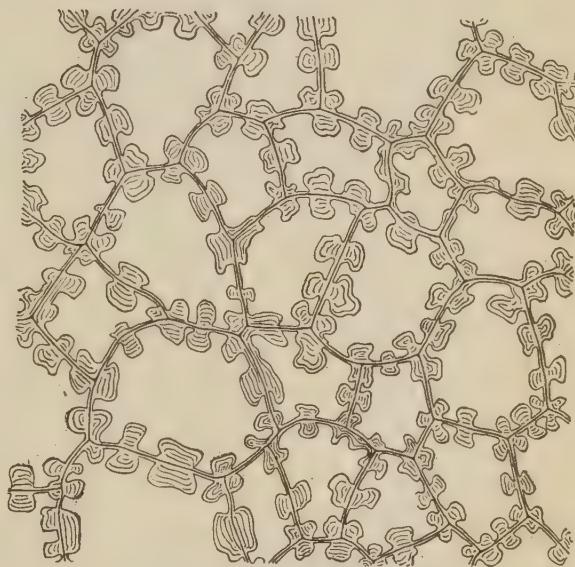


FIG. 293. Thickened walls of hemi-cellulose from betel-nut palm seed. ( $\times 140$ )

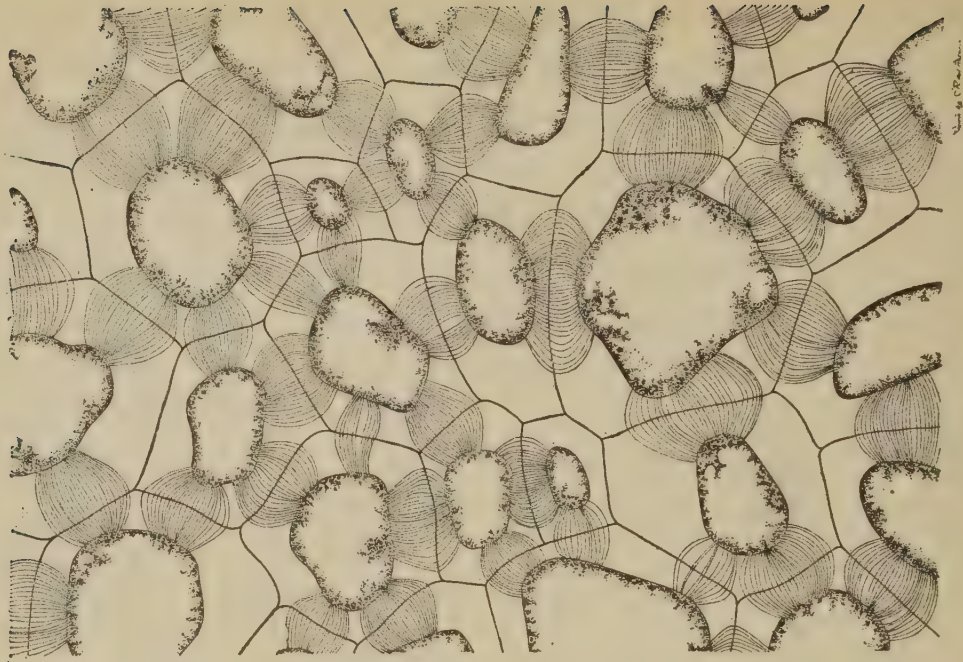


FIG. 294. Reserve cellulose in the form of thickened cell walls in the seed of the Japanese persimmon (*Diospyros kaki*)

The white areas around the cells are the cell walls. Note the fine protoplasmic connections between the cells

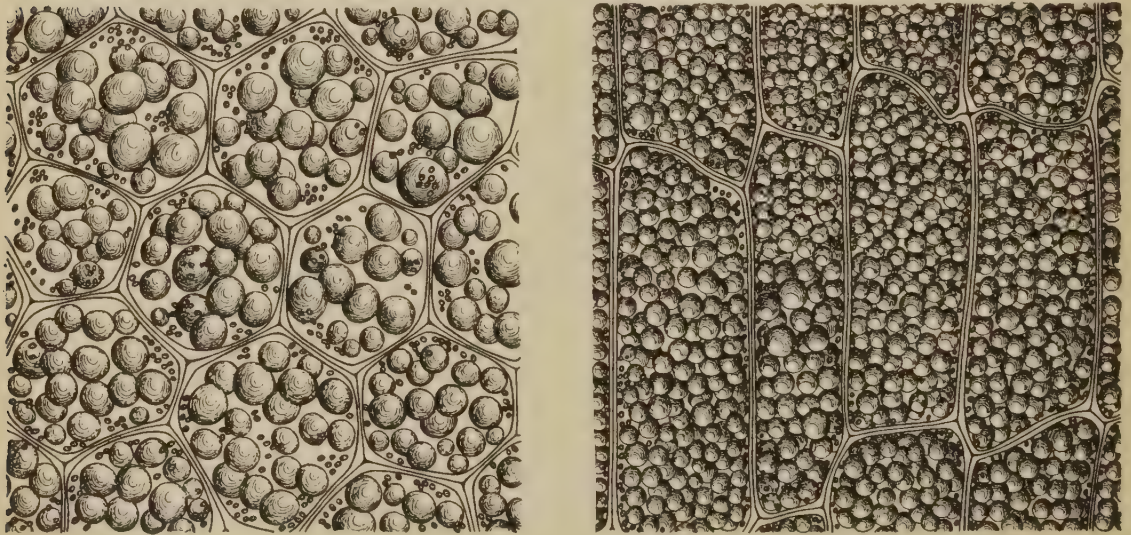


FIG. 295. Cells of endosperm (meat) of coconut

Left, cut parallel with the surface of the meat ( $\times 290$ ); right, cut perpendicular to the surface of the meat ( $\times 185$ ). The large globules are oil and the small granules are protein



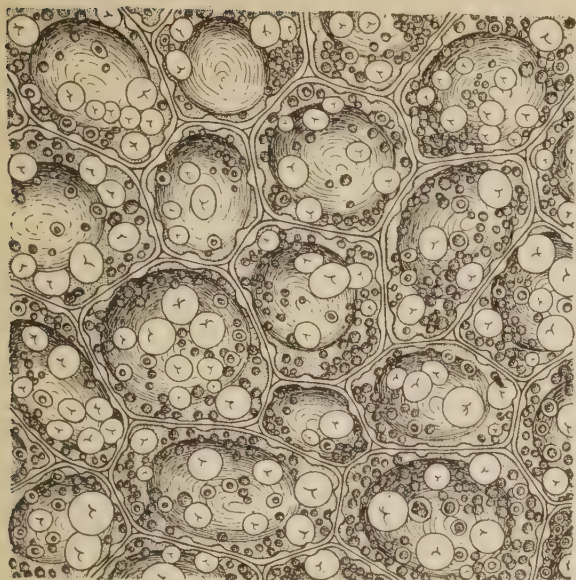


FIG. 296. Cells near the outer part of the cotyledon of peanut

The large globules are oil; the white bodies, starch grains; the small dark granules, protein; and the knoblike thickenings on the walls, hemicellulose. ( $\times 225$ )

energy, while proteins are both sources of energy and body-building materials. Vitamins, which are manufactured by plants and not by animals, are also necessary for the metabolism of animals, although they do not appear to furnish energy or to take part in the building of tissues. Vitamins are abundant in leaves.

#### DIGESTION

Food stored as starch, cellulose, fatty oil, or protein is not soluble in water, and so must be converted into a soluble form before it can be used by plants. This is accomplished by substances known as *enzymes*, which belong to the

from milk. The proteins always contain carbon, hydrogen, oxygen, and nitrogen, and many contain sulphur. Other substances, such as phosphorus, are also found in some proteins. Proteins in the form of solid granules are frequently found in plants as food-storage material (Figs. 295-298).

**Plant materials as human food.** The sugars, starches, fats, and proteins which are stored in plants are also used as food by animals, including man. The fats and carbohydrates serve as sources of en-

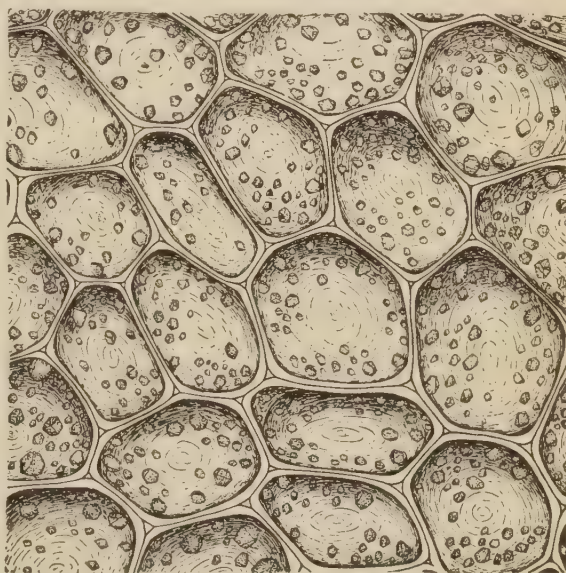


FIG. 297. Cells of lumbang nut

The granules are protein. Note how the oil fills the cells. ( $\times 265$ )



general category of catalysts. *Catalysts* are substances which change (usually accelerate) the rate of a reaction. Owing to the fact that a reaction which is accelerated by an enzyme might take place so slowly without the enzyme as to be imperceptible, it is customary, in order to avoid the use of cumbersome language, to speak of an enzyme as acting on a substance rather

than as accelerating the rate of a reaction.

Enzymes, like other catalysts, are characterized by not being a part of the initial substance in the reaction or of the final product, by not being altered in the reaction, by influencing a change in a relatively great volume of the reacting substance, and by accelerating the effect in direct proportion to the amount of catalyst present.

As an example of inorganic catalysts we may mention spongy platinum, which accelerates the oxidation of sulphur dioxide in the manufacture of sulphuric acid. Another example is finely



FIG. 298. Cells from seed of *Croton tiglium* with large, rounded oil globules and irregularly shaped protein granules. ( $\times 450$ )

divided nickel, which is used in the commercial hydrogenation of oils. By this means many inedible liquid oils are turned into solid edible fats.

Plants contain many different kinds of enzymes, and each enzyme acts on only one substance or on a group of similar substances. The best-known reactions that are accelerated by enzymes are those in which complex substances are split into simpler ones. It is believed, however, that a given enzyme can accelerate a reaction in either direction; that is, if an enzyme splits up a complex substance, it can also influence the reverse process of the building up of the same complex substance.



For simplicity we will mention only a few of the many known enzymes. *Diastase* converts starch into sugar, so that the action of this substance changes an insoluble substance into a soluble one (Fig. 299). *Invertase* changes cane sugar into glucose and fructose. *Lipase* breaks up fats into their components, glycerin and fatty acids. *Papain* splits proteins into amino acids.

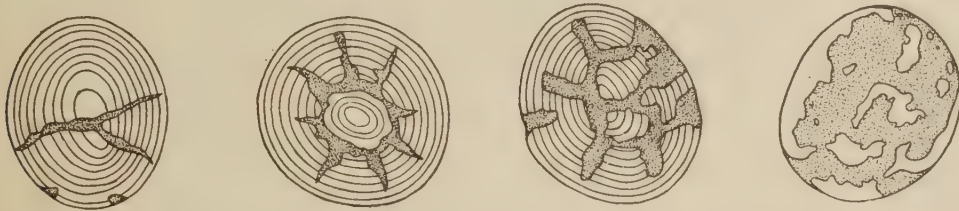


FIG. 299. Stages in digestion of starch grains of barley by diastase

Enzymes are just as important in animals as in plants. The process of digestion could not be carried on in their absence.

The chemical composition of enzymes is entirely unknown and they can be recognized only by their action; but since many of them have been prepared as dry powders, they may be regarded as chemical compounds the composition of which we may hope to know some day.

#### GERMINATION OF SEED

**Definition.** The development of the seed into a young plant is called *germination*. A seed is said to have germinated when the radicle and plumule have reached out of the seed coat, but germination is not complete until the seedling has become established and is independent of the food supply stored in the seed.

**Period of rest.** Seeds usually undergo a period of rest before germinating. The length of this period varies greatly in different species, and in some cases it is altogether lacking. In the mangrove-swamp species of the family *Rhizophoraceae* the seeds germinate without falling from the tree. The first sign of the germination of such seeds is the projection of the long, slender radicle from the fruit (Fig. 300). After the radicle has grown to a considerable length the seedling drops from the

fruit, the radicle finally becomes caught in mud, and the growth of the seedling continues (Fig. 301). While thus the growth



FIG. 300. Germinating seedling of *Rhizophora* projecting from a fruit that is still attached to a tree. ( $\times \frac{1}{3}$ )

of some embryos apparently ceases for only a very short period, if at all, most seeds in ripening lose a considerable part of their water and become comparatively dry. Under such conditions life processes continue at a very slow rate, and for practical purposes the seed is in a condition of rest. Many seeds will not begin to germinate until they have been in the state of rest for a considerable length of time, while others will germinate almost immediately.

A period during which seeds will not germinate is frequently of great advantage, particularly when the seeds are formed at the end of the growing season. In many regions the year is divided into a season which is favorable and another which is unfavorable to growth. Unfavorable seasons may be due to either very cold or very dry weather. It is obvious that if seeds began to germinate at the beginning of a long cold or long dry season, the seedlings would start under very disadvantageous conditions and would stand little chance of surviving. In regions where conditions are



FIG. 301. Seedling of *Rhizophora* after dropping from the tree and taking root. ( $\times \frac{1}{6}$ )



favorable to growth throughout the year, a prolonged period of rest is unnecessary. The seeds of many plants that are natives

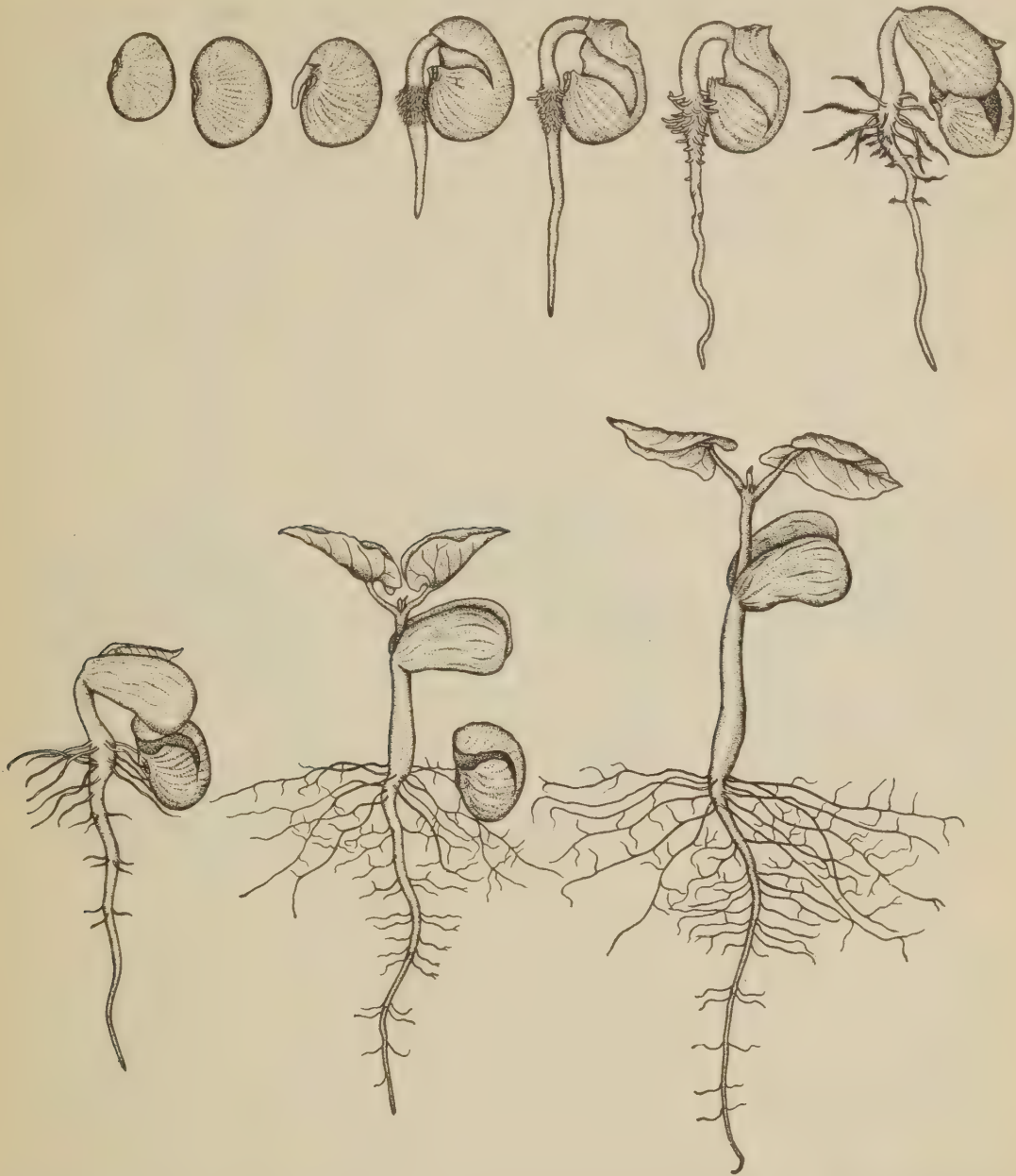


FIG. 302. Successive stages in the germination of lima bean (*Phaseolus lunatus*)

The cotyledons are carried up into the air and furnish food for the embryo, but do not become lifelike. ( $\times \frac{1}{3}$ )

of moist tropical regions germinate almost immediately, and if stored they lose their capacity for germination in a very short time.

Many seeds have hard seed coats which are impervious to water; such seeds will not germinate until the seed coats have

rotted or have been injured in some other way. This explains why the germination of many seeds is hastened by making holes in the hard seed coats. A period of rest is, however, by no means confined to such seeds as have impervious coats,

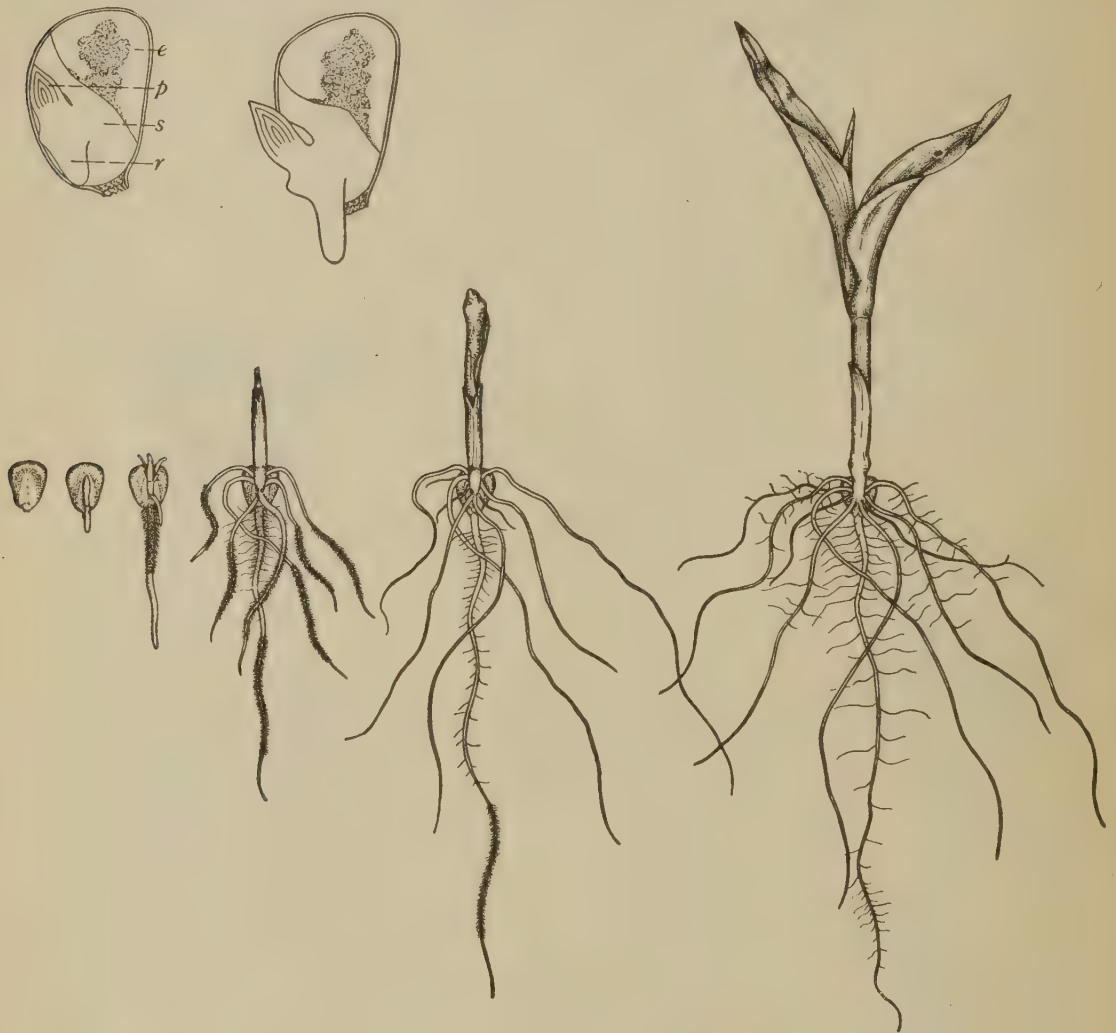


FIG. 303. Seed and germination of seedling of Indian corn

Above, section of ungerminated seed and a seed in which the plumule and radicle are pushing out: *e*, endosperm; *s*, cotyledon, or scutellum; *p*, plumule; *r*, radicle ( $\times 1\frac{1}{2}$ ). Below, germination of seed ( $\times \frac{2}{3}$ )

as the necessity for a period of rest is frequently characteristic of the seeds themselves. It would appear that some metabolic change must take place in such seeds before they are ready for germination.

Seeds in a dormant condition can withstand much greater extremes of heat and cold than can seedlings or mature plants.



**Conditions for germination.** Germination is really a process of growth, and the conditions that are necessary for germination are essentially the same as those that are required for other forms of growth. Growth is dependent on a supply of food, water, and oxygen, and a suitable temperature. Seeds normally contain sufficient food for growth, so that we do not usually think of food as a condition that is essential for germination.



FIG. 304. Successive stages in the germination of coconut

The large central meat is endosperm. In the drawing at the left the embryo is still very small; the cotyledon, which is modified as an absorbing organ, is in the endosperm, while the remainder of the embryo projects up into the husk. In the second drawing the modified cotyledon has enlarged, while the shoot appears through the husk. In the third drawing the cotyledon fills the cavity in the kernel. ( $\times \frac{2}{15}$ )

Active protoplasm consists very largely of water, while the protoplasm of dry seeds contains comparatively little water. A supply of water is therefore very essential to change the protoplasm from the relatively inactive condition in the dry seed to the active conditions in the young seedling. The amount of water absorbed is frequently considerable, and it is absorbed with great force. During the process the seeds become soft and saturated with water. This absorption of water causes most seeds to swell.

The source of energy in germination is respiration, or, in other words, the oxidation of food material stored in the seed. The amount of energy necessary is considerable, as germination requires that the material stored in the seed be rapidly transformed into tissues. Large quantities of oxygen are therefore necessary, and seeds will not germinate unless there is an

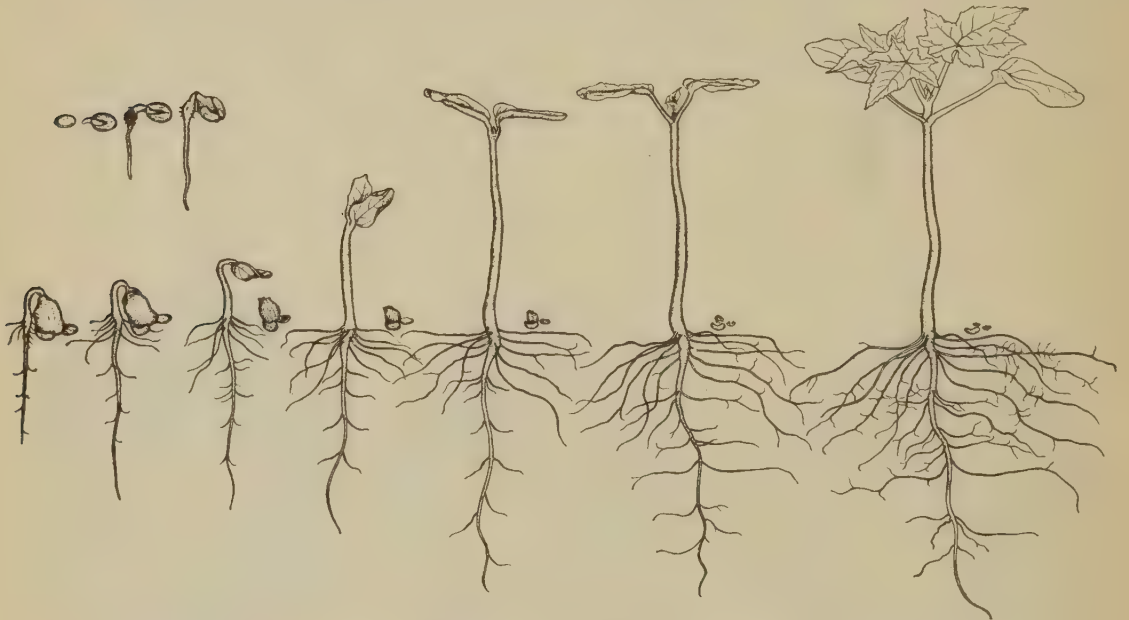


FIG. 305. Successive stages in the germination of castor-oil seed

The cotyledons first act as absorbing organs and later become green foliage leaves. Compare with Fig. 269

abundant supply. For this reason most seeds fail to germinate in poorly aërated soil, as when buried at a great depth or when the air spaces of the soil are filled with water.

**Selection of seeds.** The value of knowing the hereditary characters that are carried in a seed has already been discussed. In selecting the seeds for planting there are certain other points which it is important to take into consideration. Among these are the size and vigor of the plant producing the seed, and the size of the seed itself. Vigorous plants are more likely to produce vigorous offspring than are weak ones. Moreover, large seeds are much more likely than small ones to give rise to robust plants. A large seed indicates vigor and abundant food material for the nourishment of the young plant. Care should be taken



that seeds are fully matured. Immature seeds frequently do not germinate, or, if they do germinate, often produce weak seedlings. The age of the seed is also important. Many seeds, as we have seen, necessarily undergo a period of rest, and so can be stored for a considerable length of time without injury ;



FIG. 306. Successive stages in the germination of squash

Note the peg which catches into the seed coat and holds it while the cotyledons are pulled out. In the seed the cotyledons store food, during germination they supply food to the embryo, and later they serve as green leaves. ( $\times \frac{1}{3}$ )

but while seeds are apparently inactive, life processes are still going on, even though at a slow rate. If the seeds are stored for too long a time, they begin to lose their vitality; and this process, once started, continues until the seeds reach such a condition that they will no longer germinate.

**Germination.** The principal processes taking place during germination are the transfer of materials and growth. If the reserve food is stored in the cotyledons, it is transferred to the growing plumule and radicle (Fig. 302). When food is stored in the endosperm it is first absorbed by the cotyledons and then conveyed to the regions of growth (Fig. 303). During germination the cotyledon may therefore serve for the storage of

food, or, if the food is stored in the endosperm, as an absorbing and transferring organ.

Frequently, as in the grains of the grasses, the cotyledons serve as absorbing organs and do not leave the seeds (Fig. 303).

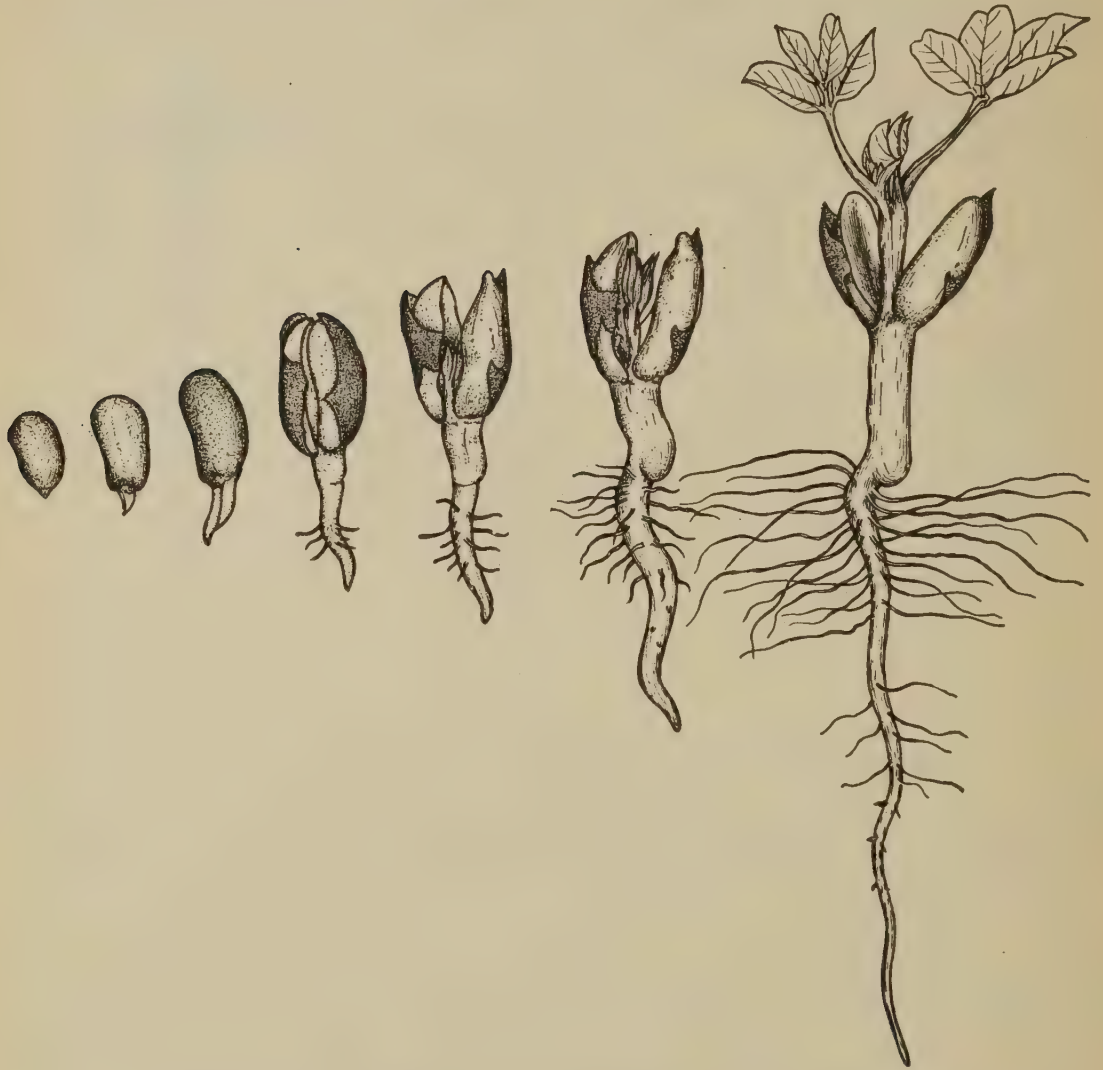


FIG. 307. Stages in the germination of peanut

The cotyledons are carried up into the air and the food transferred from them to the growing parts of the seedling, while the cotyledons shrivel without becoming green. ( $\times \frac{1}{2}$ )

The tip of the cotyledon of the coconut is modified into an absorbing organ which grows so large as to fill the cavity of the nut (Fig. 304).

In some cases in which the seeds contain endosperm (Fig. 305), and in others in which they do not (Fig. 306), the cotyledons



are carried up into the air by the growth of the hypocotyl (the part of the seedling between the cotyledon and the root) and function as green leaves. In an intermediate type the cotyledons are carried up into the air by the growing hypocotyl, but shrivel as the reserve food is exhausted and do not function as green leaves (Fig. 307). The orientation of the seedling is frequently due to movements of the cotyledons, which bend in such a way as to push the developing radicle into the ground.

## CHAPTER X

### DIVISION *THALLOPHYTA*

**Divisions of plants.** All living organisms are placed in either the plant kingdom or the animal kingdom. The plant kingdom is divided into large groups, or *divisions*, the number and size of which vary somewhat according to the opinions of different authorities. Thus what some botanists regard as one division may be divided into two or more divisions by other authorities. For convenience the plant kingdom is divided into four divisions in the following discussion. These divisions are *Thallophyta*, *Bryophyta*, *Pteridophyta*, and *Spermatophyta*.

The *Spermatophyta* are the seed plants. The *Pteridophyta* consist of the ferns and their allies. The *Bryophyta* are composed of the mosses and the mosslike plants called liverworts.

***Thallophyta.*** The name *Thallophyta* means plants with thallus bodies, that is, not differentiated into stems, roots, and leaves. The division *Thallophyta* is made up of such plants, but to say that this division contains all the thallus plants is not exact, as some of the liverworts have thallus bodies, while none of the *Bryophyta* have true roots. The *Thallophyta* include the bacteria, the algæ, the fungi, and the lichens. The algæ are the seaweeds and other simply organized water plants that have chlorophyll.

### CLASS *BACTERIA*

The bacteria are very small and apparently simply organized plants. Some of them are so small as to be just within the limit of vision of the compound microscope. There are other organisms which are so small as to be actually invisible, and it may be that some bacteria belong to this class. Most of the bacteria are either parasites or saprophytes.



**Cell structure.** The bacteria are usually divided into three groups, according to their shape: *coccus* forms, which are spherical cells; *bacillus* forms, rod-shaped cells; and *spirillum* forms, curved cells (Fig. 308).

The bacteria are small masses of protoplasm without chlorophyll and surrounded by cell walls. A few of the cocci and

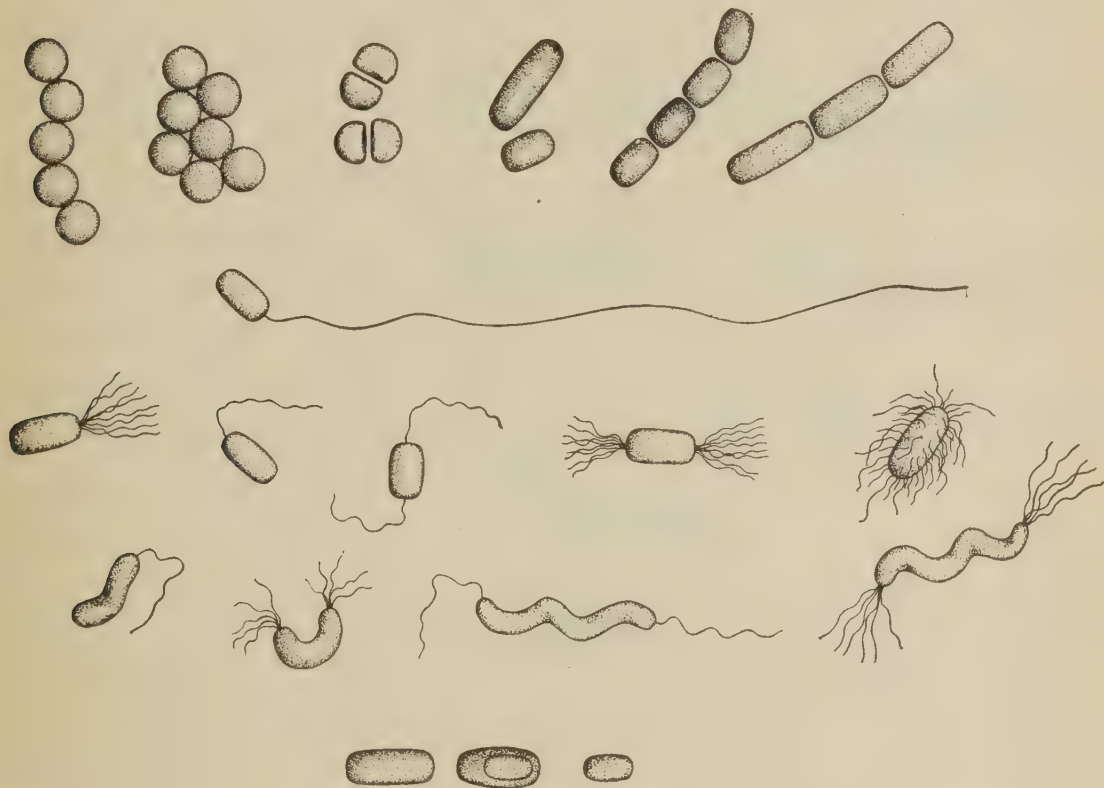


FIG. 308. Various forms of bacteria

First line, at the left, coccus forms; at the right, bacillus forms; second and third lines, bacillus forms; fourth line, spirillum forms; fifth line, stages in formation of an endospore

many of the bacilli and spirilla have very small, delicate, threadlike processes known as *flagella* (Fig. 308). The movements of these flagella give the bacteria the power of locomotion.

The bacteria do not possess nuclei such as are found in higher plants, but many of them contain granules which have staining properties resembling those of chromatin (Fig. 309). In many cases these granules are scattered throughout the cell, while single spherical, spiral, or zigzag structures have been described in some bacteria. The question as to whether or not

the bacteria have nuclei seems to depend largely on the definition of nucleus. If the term *nucleus* is confined to highly organized nuclei which divide mitotically, then the bacteria do not appear to have nuclei. If, on the other hand, granules which have staining properties resembling those of chromatin may be regarded as nuclei, some bacteria possess such structures. Certainly the bacteria do not seem to possess anything that resembles a typical nucleus.



FIG. 309. Internal structure of bacteria

Redrawn after Dobell

**Decay bacteria.** The remains of plants and animals do not decay by themselves but are destroyed by the action of other organisms. We know that fruit and meat decay very rapidly if no care is taken to prevent this process. That the decay is not due to anything inherent in the substances themselves is shown by the process of canning, as when we sterilize

milk, meat, or fruit by heat and then seal them in cans. The reason why these substances do not decay under such conditions is that by heating we kill all the living organisms that would destroy them, while by sealing we prevent the access of other organisms. Decay may be due either to bacteria or to fungi, which are also plants without chlorophyll.)

In the growth of green plants and of animals large quantities of important chemical elements are stored up in organic compounds. When plants or animals die, the elements in these organic compounds are not immediately available to green plants but must first be reduced to simple inorganic compounds. In causing the decay of organic remains and thus returning the



elements to the soil in a form in which they are available to higher plants the bacteria perform a very useful function. If it were not for the action of organisms which cause decay it is reasonable to suppose that the earth would be deeply covered by the products of the life activities of the higher organisms.

When bacteria cause the decay of substances such as wood or food which man desires to preserve, they are regarded as injurious. It should be noted, however, that in causing decay bacteria perform a function that is naturally very useful.

Bacteria sometimes produce substances that are useful to man. The souring of milk is due to the formation of lactic acid by bacteria. Vinegar is essentially a solution of acetic acid, and the so-called natural vinegar is produced by the action of bacteria that convert the alcohol of wine into acetic acid.

**Disease bacteria.** Infectious and contagious diseases are caused by small organisms that grow inside of their hosts. Some diseases are due to small animals, but the majority of the infectious and contagious diseases of man and other animals are caused by bacteria. Bacteria are responsible for such diseases as tuberculosis, typhoid fever, cholera, leprosy, plague, and pneumonia. Many diseases of plants are also caused by bacteria. There are two general ways of preventing bacterial diseases: the most obvious is to keep the bacteria from entering the host; the other method is to render the host immune to the attack of a given kind of bacteria, as by vaccination.

**Nitrogen-fixing bacteria.** Green plants obtain nitrogen from the soil in the form of compounds. Certain bacteria have the property of combining atmospheric nitrogen and fixing it in compounds that can be absorbed and used by ordinary green plants. Some of these bacteria live free in the soil. The energy which they use in fixing the nitrogen is obtained by the oxidation of carbohydrates. Other bacteria cause the growth of nodules on the roots of legumes (Fig. 310). The bacteria live in these nodules and combine the nitrogen of the air in such a way that it can be absorbed by the legumes. When such legumes die they enrich the soil with nitrogen that was fixed by the bacteria. It is

owing to this fact that land can be fertilized by growing peas or beans, especially if the plants are afterward buried in the soil.

**Reproduction of bacteria.** Bacteria reproduce by the simple division of one cell into two. The divisions frequently follow each other in rapid succession, and the length of time from one

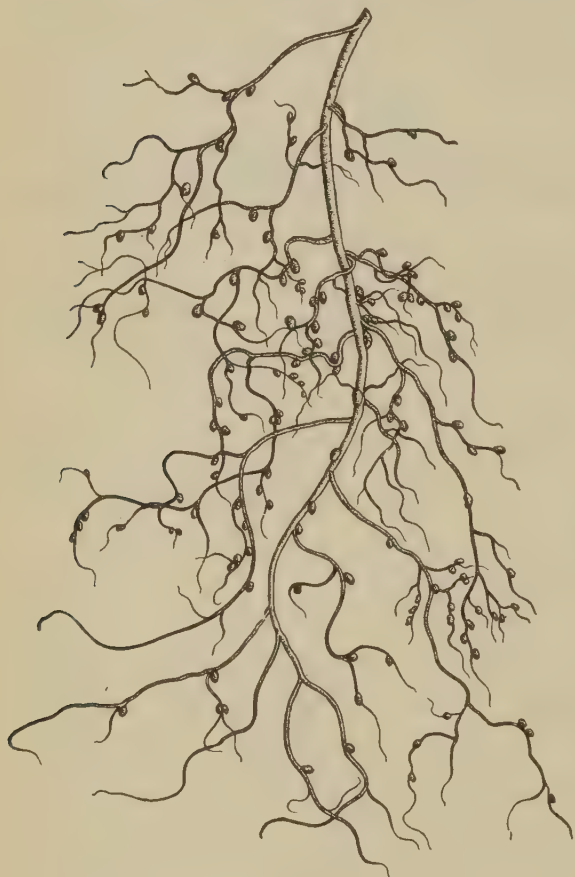


FIG. 310. Nodules on root of sensitive plant (*Mimosa pudica*) due to nitrogen-fixing bacteria. ( $\times 1$ )

division to the next may not be more than from twenty to thirty minutes. The bacilli and spirilla also produce spores. *Spores* are single-celled reproductive structures. The spores of bacteria are called *endospores* from the fact that they are formed within the cell (Fig. 308). The protoplasm of the cell surrounds itself with a thick wall within the original cell wall. The endospores are very resistant to external conditions, such as dryness or extreme temperatures. Their importance seems to lie in the fact that they enable the bacteria to survive under adverse circumstances. Under favorable conditions the covering of the

spore bursts and the protoplasm resumes its ordinary activities.

**Sources of energy.** Green plants obtain energy from sunlight and store it in the products of photosynthesis. When energy is required for the life activities of these plants, this stored energy is released by respiration, which is the oxidation of organic compounds that had their origin in the process of photosynthesis. Animals also obtain energy for their life activities by the release, through respiration, of energy stored by plants in the products of photosynthesis. The energy used by both plants



and animals, therefore, is the energy of sunlight which is stored by plants in photosynthesis. Both saprophytes and parasites resemble animals in that they obtain energy by the oxidation of organic compounds that had their origin not in themselves but in green plants. There are, however, certain kinds of bacteria that can live in the absence of both light and organic compounds. By the oxidation of inorganic mineral matter they obtain energy for all their activities, including the assimilation of carbon from carbon dioxide. These bacteria include the sulphur bacteria, which obtain energy by the oxidation of sulphur compounds, and nitrifying bacteria, which obtain energy by the oxidation of nitrogen compounds. As these bacteria can live without sunlight and in the absence of organic compounds, they give us an idea of a way in which it is possible that living organisms existed and obtained energy before the development of plants with chlorophyll.

**Relationship of bacteria.** The bacteria have the simplest structure of all known living organisms. Moreover, since there are bacteria that can live in the absence of light and of organic compounds, and so have a method of obtaining energy which could have been used by plants before the evolution of chlorophyll, and since some of the oldest sedimentary rocks show evidence of bacterial action, there are grounds for the opinion that the bacteria are the most primitive of known living organisms.

While the bacteria are a very primitive group, it does not follow that all the individual species are ancient. Indeed, those that naturally live only in the human body would appear to be of recent origin, as they have physiological properties which they could hardly have acquired before the advent of man, or of animals rather closely related to him.

#### GENERAL SURVEY OF ALGÆ

Most of the simpler chlorophyll-bearing plants are known by the popular name of *algæ*. Algæ include four classes: the blue-green algæ, the green algæ, the brown algæ, and the red algæ, the designations referring to the colors of the groups. The blue-green

algæ are generally believed to be the most primitive, while the other three groups are usually considered to be descended from a class of unicellular organisms that are known as flagellates.

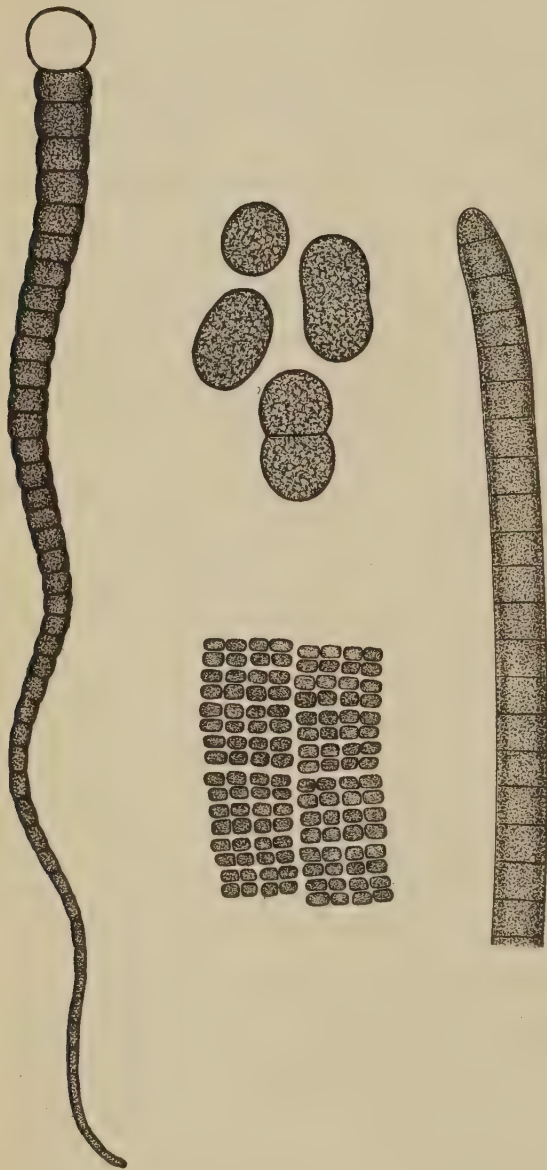


FIG. 311. Forms of blue-green algæ  
Left, *Rivularia*; upper center, *Aphanothece*; lower center, *Merismopedia*;  
right, *Oscillatoria*

*Blue-green algæ* are the most simply organized of chlorophyll-bearing plants. The individuals consist either of single cells, rows of cells, or colonies of cells (Figs. 311, 312). In this group no method of sexual reproduction is known; propagation results from the division of cells. The class as a whole is characterized by the absence of a definite nucleus and mitotic division, although in the higher members there is a central body, frequently called an incipient nucleus, whose structure approaches that of a nucleus. Also, the chlorophyll is not aggregated into plastids but is diffused in the peripheral portion of the protoplasm. While the blue-green algæ are the most simply organized plants with chlorophyll, there is great uncertainty as to how they may be related to other chlorophyll-bearing plants.

The *flagellates* are believed to be the ancestors of the true algæ, which include the green, the brown, and the red algæ. The flagellates (Fig. 317) are single-celled organisms which move by means of long, slender, protoplasmic projections called flagella. The green flagellates contain chloroplasts and a



well-developed nucleus; in these features they are much more advanced than the blue-green algæ. Propagation is by means of the division of a cell (Fig. 319), no sexual reproduction being known.

The most primitive of the *green algæ* are somewhat more advanced types of unicellular plants, which, like the flagellates, move by means of flagella (Fig. 320). In these there are two types of reproduction. The cell contents may divide (Fig. 322) to form a number of small individuals, or *zoöspores*, which are like mature individuals except in size, and which, without sexual fusion, grow into mature individuals; or the cell contents may divide into a somewhat larger number of smaller bodies, or *gametes*, which have the same structure as zoöspores, but which fuse in pairs to give rise to new individuals (Fig. 323). Reproduction by fusion of two similar gametes is a very simple form of sexuality.

In somewhat higher types of plants sexual reproduction may be

due either to the fusion of similar gametes or to the fusion of a large and a small gamete (Fig. 328), while in still more advanced types the large gametes become nonmotile eggs which are fertilized by small gametes called spermatozoids (Figs. 331, 333).

Just as the algæ show an evolution in the development of sex, they also exhibit a gradual development of a nonmotile vegetative body. One of the most primitive indications of a nonmotile vegetative body is found in certain primitive, motile, unicellular forms of green algæ. In these, under certain conditions, the individuals may withdraw their flagella and by division give rise to a colony of nonmotile cells held together by a gelatinous matrix (Figs. 320, 321). When conditions again become favorable for the motile state, the cells send out flagella

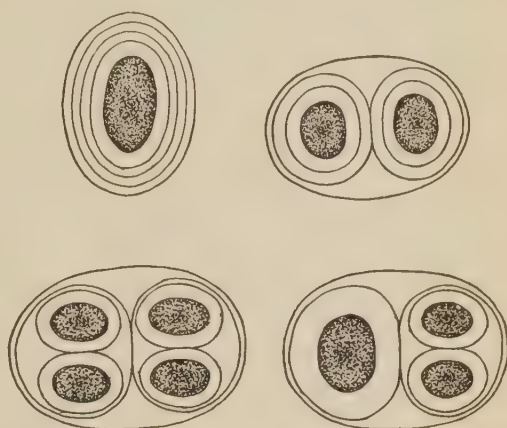


FIG. 312. *Gloeocapsa*

A single-celled individual and colonies of two, three, and four cells.  
( $\times 1285$ )

and swim out of the gelatinous material. The colonial development just described may be regarded as an indication of a non-motile, vegetative development interpolated between motile states. In somewhat more advanced types motile reproductive cells give rise to vegetative bodies consisting of rows of cells (Fig. 327), and these in turn reproduce by means of motile cells which resemble the mature individuals of the primitive, unicellular, motile forms (Fig. 328). The vegetative body here also may be regarded as being a development of a nonmotile state interpolated between motile states. In the higher algæ the interpolated vegetative body becomes very complex (Fig. 335), while the portions which bear gametes are highly specialized (Fig. 336).

In the algæ there has been more than a single development of sexuality; they have developed from the fusion of similar gametes to the fertilization of eggs by spermatozoids, and this development has taken place independently along a number of different lines (Figs. 343, 353). The development of a complex vegetative body has also occurred independently along different lines, with the result that there is great variation in structure among the algæ (Figs. 325, 339, 342, 344, 345, 348, 350, 352, 354).

#### CLASS *CYANOPHYCEAE* (BLUE-GREEN ALGÆ)

The members of this class are very simple plants. The individuals consist of single cells, of colonies of cells held together by a gelatinous covering, or of chains of cells (Figs. 311-314). The popular name, *blue-green algæ*, refers to the characteristic blue-green color of these plants.

**Cell structure.** The *Cyanophyceae* contain chlorophyll and in addition the blue pigment phycocyanin.

The cells are characterized by having a colorless central portion, the so-called *central body*, surrounded by a pigmented zone. The central body seems to represent an incipient nucleus, but is not separated from the remainder of the cell by a membrane, while its structure is certainly much more primitive than that



of an ordinary nucleus. The complexity of this incipient nucleus varies greatly in different forms. In the most advanced types it is clearly differentiated from the remainder of the protoplasm, while in the simplest forms such differentiation has not been demonstrated.

The group as a whole is characterized by having the photosynthetic pigment distributed in the peripheral zone, and not collected in chloroplastids as in the higher plants.

Another very characteristic feature of the *Cyanophyceae* is the gelatinous coverings that surround them. The gelatinous coverings and the blue-green color give the *Cyanophyceae* their characteristic appearance, as they can usually be recognized as slimy, blue-green masses.

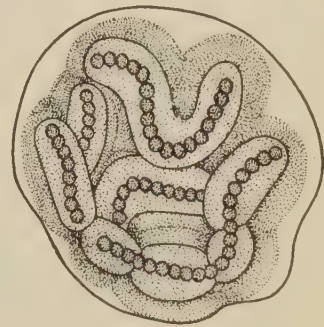
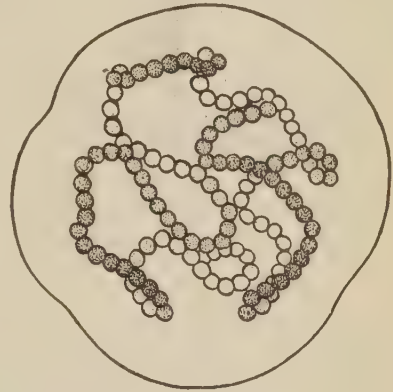


FIG. 314. Two species of *Nostoc*, each embedded in a gelatinous matrix



FIG. 313. A single cell of *Spirulina*, a blue-green alga. ( $\times 925$ )

In those species in which the plant consists of a single cell or a colony of cells held together by mucilaginous materials all the cells are alike, and in

many of the species in which the cells are arranged in the form of chains the cells are alike. In other species there are special cells called *heterocysts* (Figs. 315, 316). These are formed from ordinary cells, usually by increase in size and an almost complete loss of pigment.

**Reproduction.** The *Cyanophyceae* have no method of sexual reproduction. The single-celled and colonial forms are reproduced by simple division. In the filamentous species vegetative

reproduction is often due to the breaking up of the filament into short pieces called *hormogonia*, which are often limited in size by heterocysts. Reproduction may also be due to the formation of

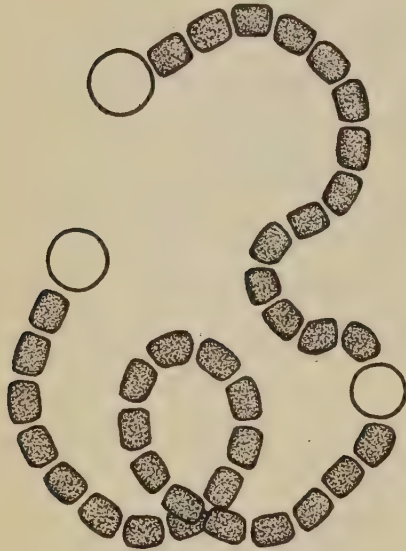


FIG. 315. A filament of *Nostoc* with heterocysts. ( $\times 695$ )

resting spores. A *spore* is a one-celled reproductive structure. In all cases the resting spores of the *Cyanophyceae* arise from ordinary cells, which generally increase in size and become largely filled with stored food materials and surrounded by two distinct membranes. **Distribution.** The *Cyanophyceae* are found in all parts of the world. They usually occur in water or in damp localities, but also occur in dry situations. They are frequently very abundant in fresh water and sometimes occur in such quantities as to produce a distinct color, the so-called "water blume." Cattle may be killed by drinking such water. When the *Cyanophyceae* occur in water in great quantities, their death and decay frequently gives the water a very unpleasant odor and taste.

**Relationship of *Cyanophyceae*.** The apparently simple structure of the cell of the *Cyanophyceae* and the absence of a sexual method of reproduction indicate that they are very primitive forms of plants. The bacteria, which lack chlorophyll, are the only other plants that do not have definite nuclei, while the *Cyanophyceae* are the only plants with chlorophyll that do not have chloroplastids. For these reasons the *Cyanophyceae* are regarded as the most primitive chlorophyll-bearing plants.

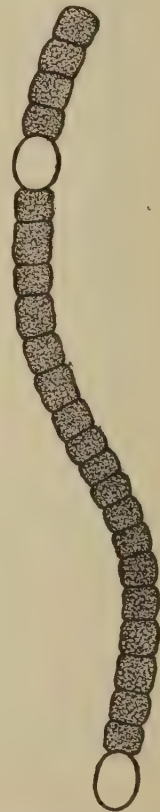


FIG. 316. *Anabaena* with heterocysts. ( $\times 535$ )



It seems reasonable to suppose that the most primitive ancestors of the higher plants lacked a definite nucleus, and also that they did not have a method of sexual reproduction. Moreover, it would seem highly probable that the first plant that possessed chlorophyll did not have definite chloroplastids. It appears, therefore, that the *Cyanophyceae* possess many features that must have been characteristic of some of the primitive ancestors of the higher plants. While there is no evidence that the *Cyanophyceae* themselves gave rise to any higher group, it does seem probable that they and the higher plants had at least a common ancestor, and that in many respects the *Cyanophyceae* resemble this common ancestor very much more than do the higher plants.

The only close relationship of the *Cyanophyceae* is to the bacteria, which they resemble in lacking sexuality and a highly organized nucleus and in the method of cell division.

#### CLASS FLAGELLATA

The flagellates consist of unicellular or colonial aquatic organisms which have both animal and plant characteristics. The name *Flagellata* refers to one or two (rarely more) slender, hair-like projections called *flagella*, the movement of which enables the individuals to swim in water (Fig. 317).

**Cell structure.** The cell is naked or has a distinct membrane which seldom contains cellulose. Within a cell is a single nucleus and a pulsating vacuole, while many species have a red eyespot (Fig. 317). Some forms have well-developed green, yellow, or brown plastids which enable them to carry on photosynthesis; others are colorless and live by absorbing organic matter from the surrounding water; while many can take in and digest solid particles. Some forms contain chlorophyll and manufacture food by photosynthesis when living in the light (Fig. 318), but when growing in the dark in nutrient solutions they lose their chlorophyll and absorb organic food from the surrounding medium (Fig. 318).

**Reproduction.** Flagellates are reproduced by the longitudinal division of the cell (Fig. 319), no sexual reproduction being known. In many species the cell may become rounded and inclosed in a thick cell wall, forming a resting spore (Fig. 318). The protoplast, on germination, divides to form a number of new individuals (Fig. 318).

**Euglena.** This is a very common and well-known genus of the *Flagellata* (Figs. 317, 319), which is frequently so abundant



FIG. 317. *Euglena* showing various forms assumed by a single cell. ( $\times 675$ )

in small puddles of standing water as to give the water a greenish color. *Euglena* has a single flagellum which enables it to swim through the water, but it can also crawl by means of movements which change the shape of the cell. In its usual form it has bright-green chloroplastids, but when grown in the dark in nutrient solutions it loses its chlorophyll and lives in the same manner as do many unicellular animals (Fig. 318). It reproduces either by longitudinal fission (Fig. 319) or by the division of the protoplast of rounded cysts or spores (Fig. 318) to form new individuals.



**Relationship of *Flagellata*.** The flagellates are a very interesting group; they are clearly on the border line between animals and

plants, and there are reasons for considering them as the group from which both animals and higher plants have been derived.

While at least those forms which contain chlorophyll may surely be regarded as plants, the whole group is considered by zoölogists as belonging to the animal kingdom, and those forms that

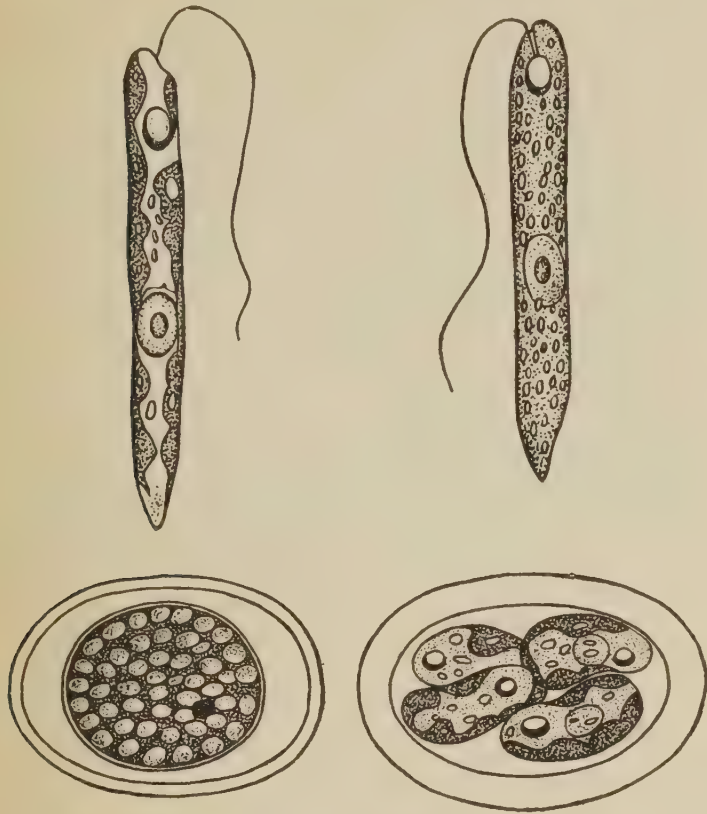


FIG. 318. *Euglena gracilis*

Upper left, green form; upper right, colorless form grown in nutrient solution in the dark; lower left, resting spore; lower right, contents of resting spore divided to form four daughter cells. (Redrawn after Zumstein)

lack chlorophyll are certainly like animals in their characteristics. A way in which protozoa (one-celled animals) may have been derived from plants is suggested by those forms which contain chlorophyll and at the same time ingest solid food particles, and by those which under certain conditions contain chlorophyll and obtain food by photosynthesis and under other conditions lack chlorophyll and live like animals.

Some of the characteristics of the flagellates which at first sight might seem to suggest that they are animals are the very

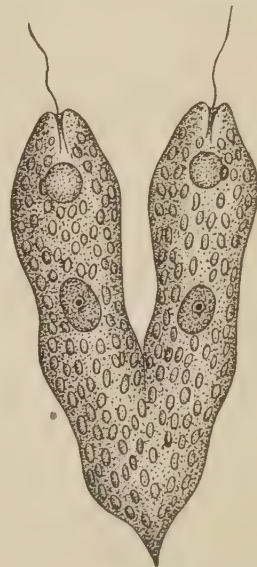


FIG. 319. Division of motile cell of *Euglena*  
Redrawn after Stein

ones that indicate most clearly that they are the ancestors of the higher plants. Movement by means of flagella is found in



FIG. 320. *Chlamydomonas*

Near the upper end in the clear area are two contractile vacuoles. Most of the cell is colored by a chloroplastid. In the upper right part of the cell is a pigment spot, eyespot. ( $\times 1300$ )

the simplest plants, the bacteria, and is characteristic of the simpler algæ, while similar types of movement are found in sexual cells of specialized plants even as high in the evolutionary scale as the simplest of the seed plants. Likewise, the presence of an eyespot is characteristic of many of the unicellular plants and of the sexual cells of some of the multicellular ones. A consideration of the flagellates shows very clearly that there is no absolute distinction between plants and animals.

It seems reasonable to suppose that the flagellates were derived from some simpler chlorophyll-bearing plants. The *Cyanophyceae*, however, are the only known chlorophyll-bearing plants which are considered as more primitive than the *Flagellata*, and the way in which these two groups may be related is entirely uncertain.

#### CLASS CHLOROPHYCEAE (GREEN ALGÆ)

Green algæ are more varied in form than any other group of plants, and it is evident that they have undergone evolution along a number of different lines. To acquire any clear conception of the different subdivisions of the green algæ would be impossible in a short course. For this reason, in the following discussion no attempt is made to deal with the classification of the green algæ or to do more than indicate a few lines of evolution. The forms described have been selected because they are common and widely distributed; and show something of the diversity of green algæ and the evolution of sex



CHLAMYDOMONAS

**Cell structure.** The genus *Chlamydomonas* is an interesting unicellular form which is clearly intermediate between the flagellates

and many of the higher green algæ. The cells of *Chlamydomonas* are spherical, oval, or somewhat cylindrical. They are surrounded by cell walls, and each individual has two cilia or flagella at its anterior end (Fig. 320). The term *cilium* is more inclusive than *flagellum*, a flagellum being a long, mobile cilium.

The protoplasm at the anterior end is clear

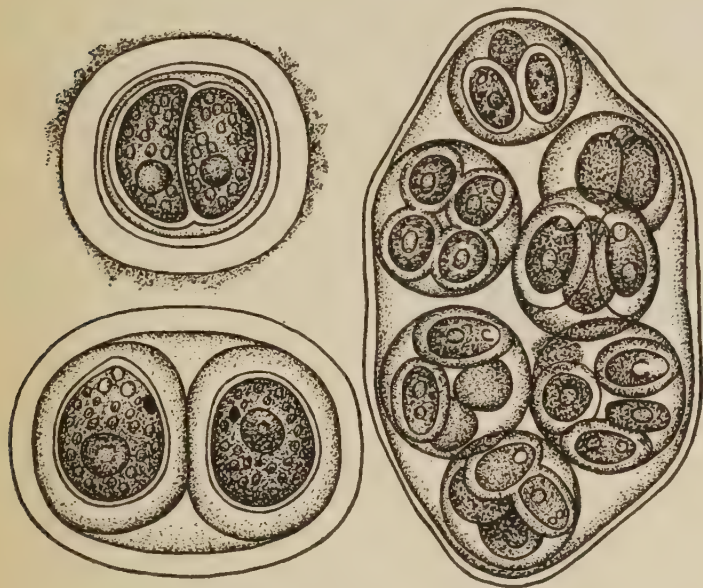


FIG. 321. Palmella state of *Chlamydomonas*  
Redrawn after Goroschankin from Oltmanns

and contains two pulsating vacuoles. Most species of *Chlamydomonas* have a red spot, called the eyespot, which is usually at the anterior end. The cell contains a chloroplastid which, typically, is cup-shaped and contains a pyrenoid. *Pyrenoids* are found in the chloroplastids of many green algæ and usually consist of a central protein portion surrounded by starch. In many cases the pyrenoids seem to be connected with the formation of starch.

*Chlamydomonas* has what is known as a *palmella* stage, during which it loses its cilia and may divide to form numerous

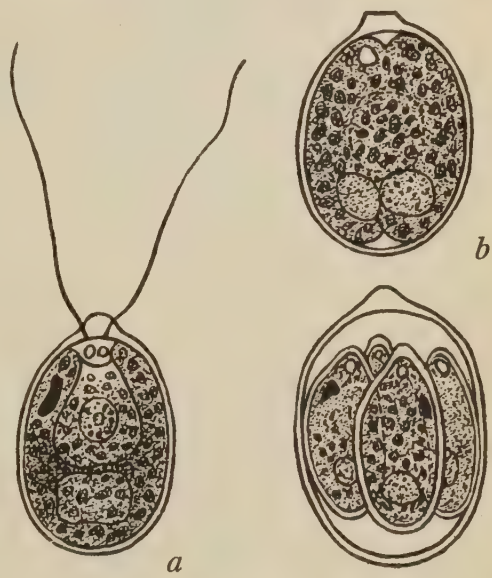


FIG. 322. Division of *Chlamydomonas angulosa* into daughter cells  
Redrawn after Dill

individuals held together by a gelatinous envelope (Fig. 321). When conditions again become favorable to the motile stage, the cells acquire cilia and swim out of the jelly.

**Reproduction.** *Chlamydomonas* reproduces vegetatively by the formation of zoöspores, a method which is characteristic of many

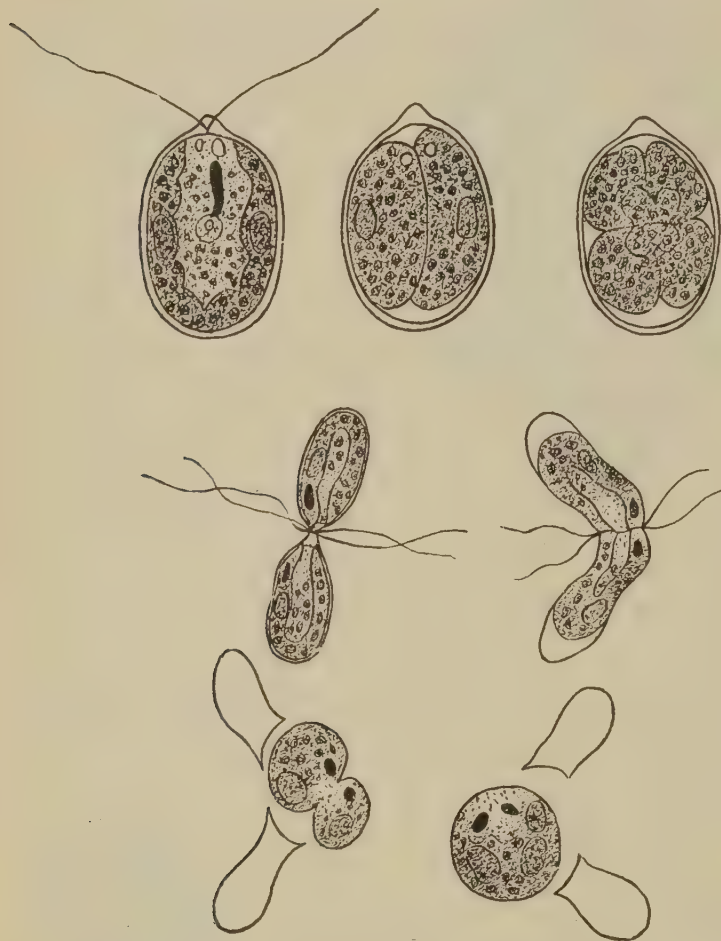


FIG. 323. *Chlamydomonas longistigma*

Above, division into daughter cells; lower figures show the conjugation of gametes. (Redrawn after Dill)

green algæ. Zoöspores are motile spores. In the formation of zoöspores in *Chlamydomonas* the contents of the cell divide rapidly into two, four, or eight parts (Fig. 322). These acquire the structure of mature individuals and are set free from the mother cell by the conversion of the wall of the latter into mucilaginous material. The mature motile individuals are simply enlarged zoöspores.

Sexual reproduction takes place by means of gametes, which are formed in the same way as zoöspores and have the same general structure, but are frequently smaller and more numerous (Fig. 323). Two of these fuse together to form a single cell known as a zygospore. A *zygospore* is a spore formed as a result of the fusion of two similar gametes. The zygospore surrounds itself with a thick wall and undergoes a period of rest. When conditions are favorable, the contents of zygospores are transformed into zoöspores, which enlarge and

Sexual reproduction takes place by



become mature motile individuals. In most cases the gametes of *Chlamydomonas* are all alike (isogametes), while in some cases they differ in size (heterogametes).

The similarity of the gametes and zoöspores of *Chlamydomonas* indicates that in such cases gametes have been derived from zoöspores and that sexuality had its origin in the transformation of non-sexual zoöspores into sexual gametes.

**Relationship of *Chlamydomonas*.** The eyespot, the contractile vacuoles, and the flagella of *Chlamydomonas* are distinctive structures which are also presented by the flagellates. The fact that these structures are found in both *Flagellata* and *Chlamydomonas* indicates that the groups are very closely related. *Chlamydomonas* is more advanced than the *Flagellata* in that it has a sexual method of reproduction.

### ULOTHRIX

**Vegetative structure.** *Ulothrix* is a green alga which is frequently abundant as a hairy growth on stones in

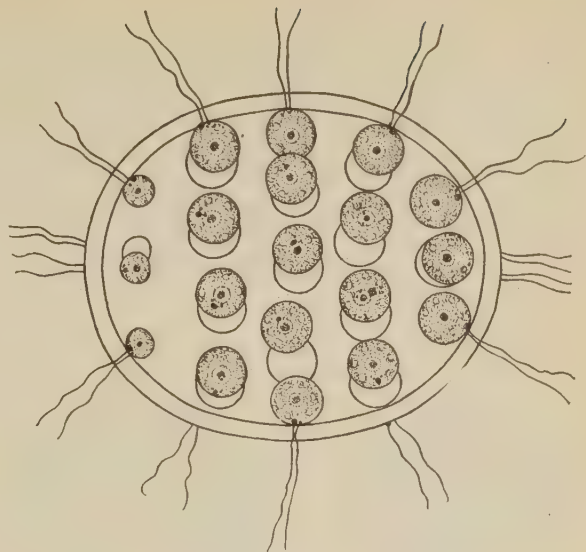


FIG. 324. *Pleodorina illinoisensis*

This is one of the simpler members of the family *Volvocaceae*, in which the individual cells are arranged in colonies in the form of a hollow sphere. Vegetative reproduction is by the division of a single cell to form a colony. Asexual reproduction in the lower forms is by isogametes. Compare with Fig. 325. (After Kofoid) ( $\times 250$ )

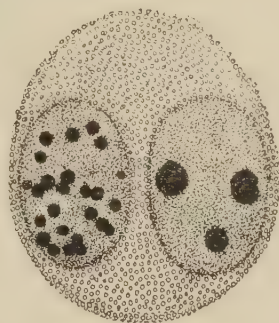


FIG. 325. *Merrillosphaera africana*

This is one of the higher members of the family *Volvocaceae*, in which a colony consists of many cells and in which sexual reproduction is by the union of eggs and sperms. Within the mother colony are two large daughter colonies. The daughter at the left contains twenty-three eggs and two groups of sperm cells, which are at the right and left. The daughter at the right contains three asexual granddaughter colonies. (After W. R. Shaw)

slow-running streams, ponds, etc. The vegetative plant consists of a row of cells which are similar except that the lower one serves to attach the plant to the substratum. Each cell contains a single nucleus and a single large chloroplastid (Fig. 327).

**Reproduction.** Asexual reproduction takes place by means of zoöspores with two or four cilia (Fig. 328). Each zoöspore has



FIG. 326. *Protococcus*, a green alga which is common as a green coating on tree trunks and stone walls

*Protococcus* consists of either a single cell or a colony of cells. Each cell contains a nucleus and a single chloroplastid. ( $\times 2470$ )

FIG. 327. Cell from filament of *Ulothrix*

Note that each cell contains a single nucleus and a band-shaped chloroplastid. ( $\times 462$ )

a red eyespot and a chloroplastid. The zoöspores are formed in ordinary vegetative cells by the division of the protoplasm into a number of separate parts which acquire the characters of zoöspores. The zoöspores escape through an opening in the cell wall and, after swimming for a time, come to rest and grow into new plants (Fig. 328).

Sexual reproduction is by means of gametes. These are produced in the same way as the zoöspores and in structure are like the zoöspores except that the gametes never possess more



than two cilia, are smaller than zoöspores, and are produced in larger numbers in a cell (Fig. 328). The gametes fuse in pairs to form zygospores, each of which becomes surrounded by a cell wall (Fig. 328). After a period of rest the zygospore germinates and produces a small, single-celled plant, the protoplast of which

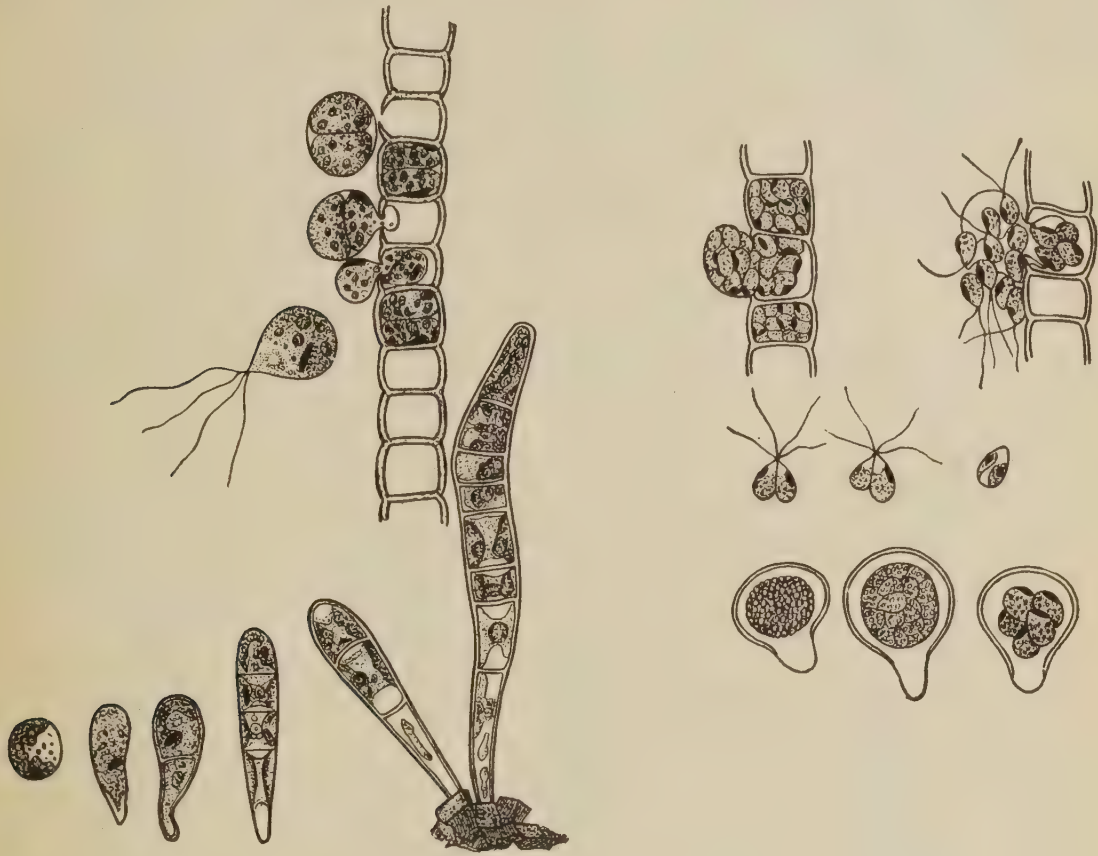


FIG. 328. *Ulothrix*

Left: above, the formation of zoöspores; below, germination of zoöspores. Right: upper line, formation and escape of gametes; middle line, conjugation of gametes; lower line, germination of gametes with the reproduction of zoöspores. (Redrawn after Dodel-Port)

divides to form a number of zoöspores, which, like other zoöspores, grow into ordinary vegetative plants (Fig. 328). Under certain conditions gametes may germinate without fusion.

The fact that the gametes are similar to zoöspores and that gametes may germinate without fusion indicates, as in the case of *Chlamydomonas*, that gametes are modified zoöspores and that sexuality may have resulted from a change of nonsexual zoöspores into sexual gametes.



FIG. 329. *Pediastrum*,  
a colonial green alga.  
( $\times 210$ )

In the same species of *Ulothrix* there may be a fusion of similar gametes, and in that case there is no differentiation of sexes; or there may be a fusion of microgametes (small gametes) and megagametes (large gametes), which indicates an early state of differentiation of sexes.

**Relationship of *Ulothrix*.** The similarity of the reproductive cells of *Ulothrix* to the mature individuals of such forms as *Chlamydomonas* and the *Flagellata* indicates that *Ulothrix* was derived from a flagellate ancestor. The vegetative plant of *Ulothrix* may be regarded as interposed between motile states in the same way as the palmella state is interposed between motile states in *Chlamydomonas*.

#### OEDOGONIUM

##### Vegetative structure.

*Oedogonium* is a very common genus of fresh-water algæ. A plant consists of an unbranched filament which when young is attached to the substratum by means of a basal cell. When the filaments become older they may float freely in the water. Each cell contains a single nucleus and a single large chloroplastid, which is composed of anastomosing strands.

**Reproduction.** Asexual reproduction is by means of zoöspores which are formed singly in vegetative cells (Fig. 330). The

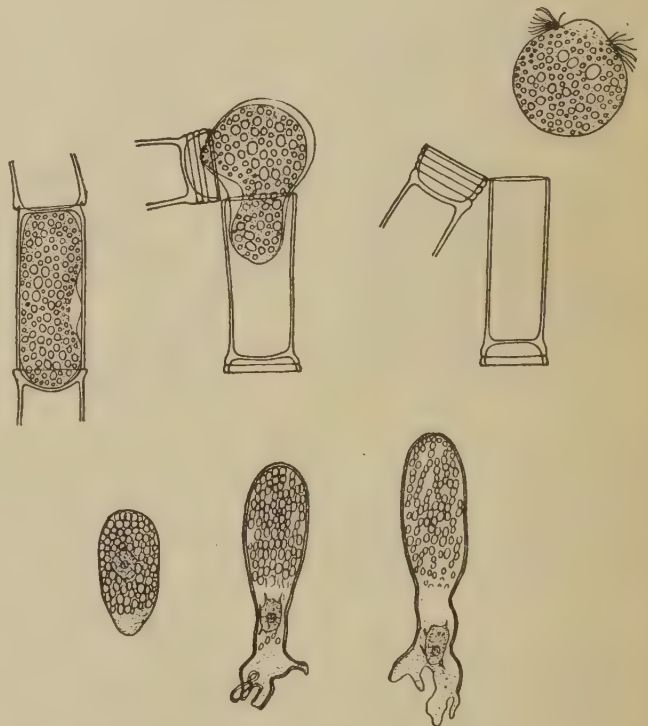


FIG. 330. *Oedogonium*

Above, formation and escape of zoöspore; below, germination of zoöspore. (Redrawn after Hirn)



zoöspore is an egg-shaped structure (Fig. 330). The anterior region is clear and is surrounded by a circle of cilia, while the remainder of the zoöspore is colored green by the chloroplastid. The zoöspore sometimes contains a pigment spot. A zoöspore is set free by the splitting of the wall of the cell in which it is produced. It swims about for a while, then attaches itself to some object by means of its anterior end, withdraws its cilia, produces a cell wall, and grows into a new filament (Fig. 330).



FIG. 331. Filament of *Oedogonium*

Below is a large rounded oogonium, and above are four small cells, the antheridia. ( $\times 240$ )

Sexual reproduction is the result of the fusion of an *egg* and a *spermatozoid*. A *spermatozoid* is a small motile gamete which fuses with an egg. The eggs are borne singly in large, rounded cells known as oögonia (Fig. 331), while the spermatozoids are formed in special small cells called antheridia (Fig. 331).

An *oögonium* is a structure in which one or more eggs are produced, while an *antheridium* is a structure in which spermatozoids are formed. The spermatozoids are similar to the zoöspores except that they are smaller. When the egg is ready for fertilization, an opening appears in the wall of the oögonium, and the spermatozoid enters through this and fuses with the egg cell (Fig. 333).

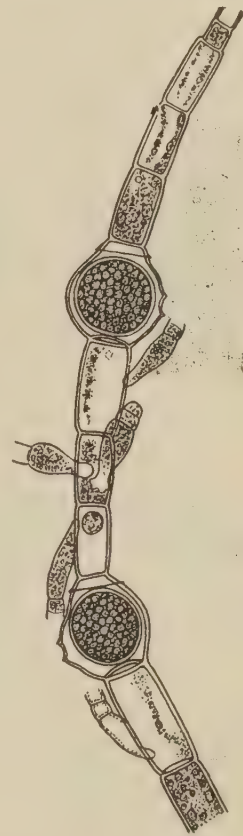


FIG. 332. Plant of *Oedogonium* with two rounded oögonia and five dwarf males attached to it

Redrawn after Pringsheim

The fertilized egg then surrounds itself with a thick wall and becomes a resting spore. This spore is known as an *oöspore*, as

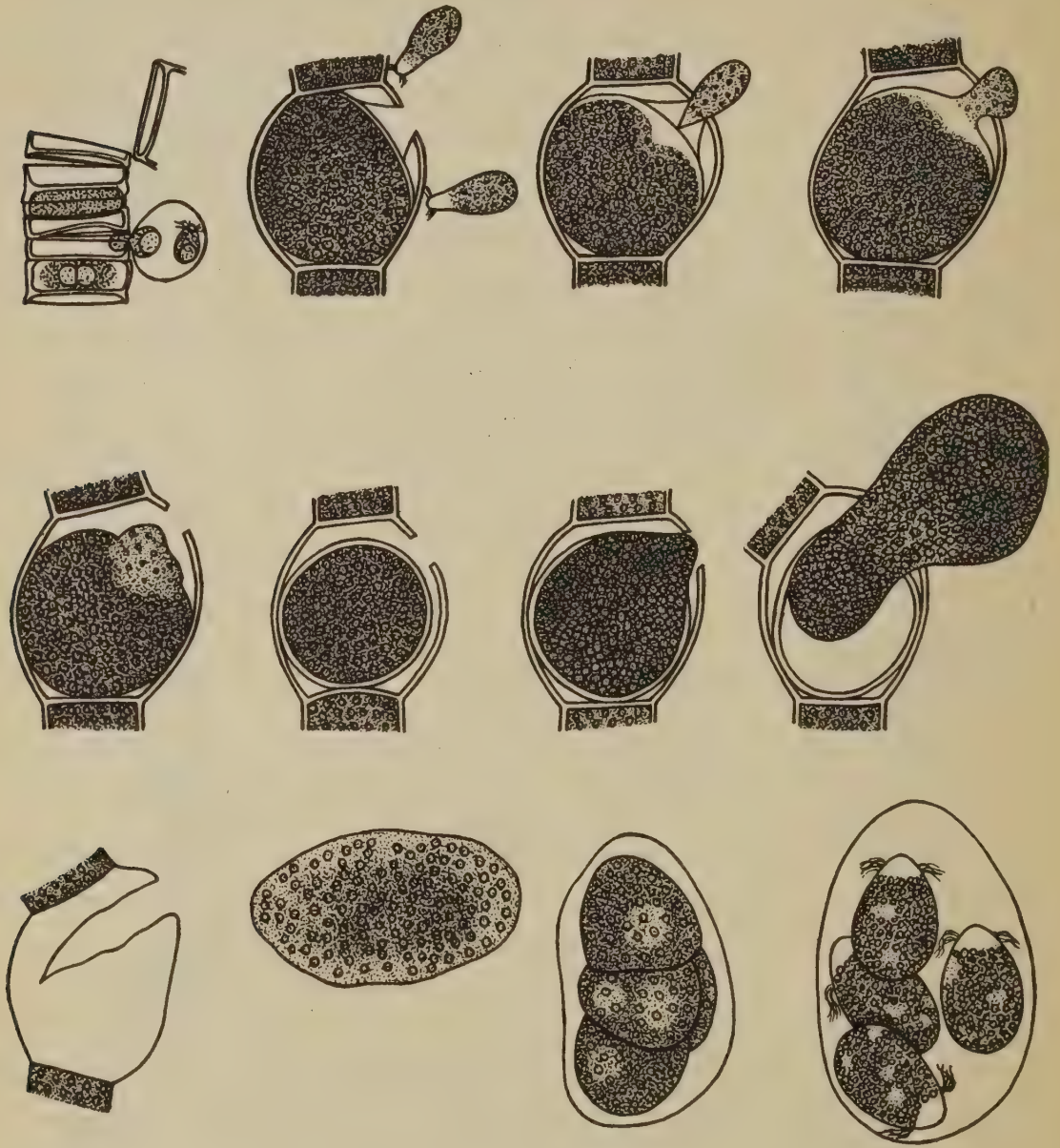


FIG. 333. *Oedogonium*

The first figure represents the escape of spermatozooids; the next four, fertilization; the sixth figure, oöspore; the seventh to ninth figures, escape of contents of oöspore; the last two figures, formation of zoöspores. (The first figure redrawn after Hirn; the remainder redrawn after Juranyi)

it is produced by the fertilization of an egg. When it germinates, the protoplasm divides to form four zoöspores (Fig. 333).

In some species the antheridia occur in ordinary vegetative filaments (Fig. 331); in other species they occur in dwarf male



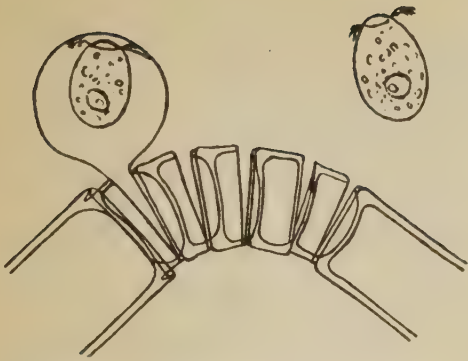


FIG. 334. Escape of androspores of *Oedogonium*  
Redrawn after Hirn

plants (Fig. 332). When the antheridia are formed in ordinary filaments, they usually occur as rows of small cells, each of which produces two spermatozoids. Dwarf male plants are developed from special spores known as *androspores*, which are very much like the zoöspores but are formed in rows of small cells (Fig. 334). These androspores attach themselves on or near the oögonia, and each grows into a dwarf male which consists of only one or a few cells.

**Relationship.** *Oedogonium* shows a very high degree of sexual differentiation, as fusion takes place

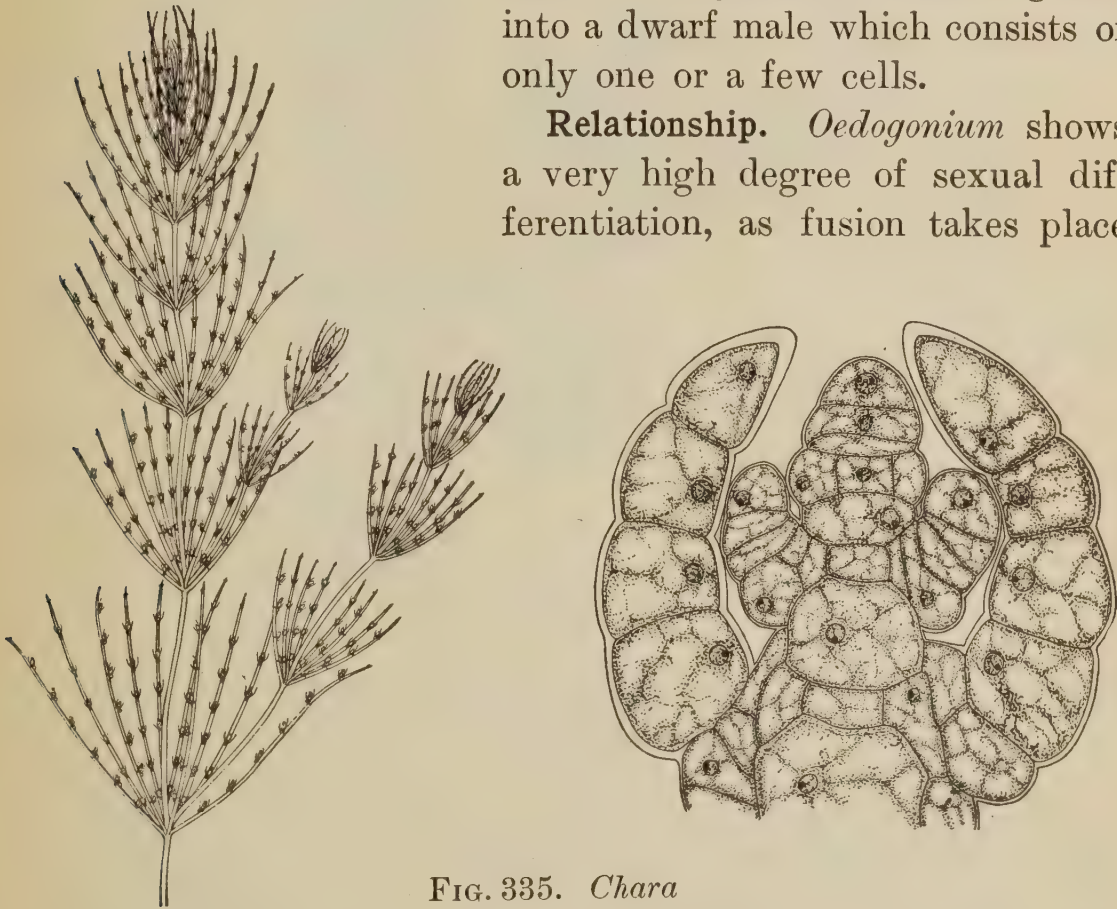


FIG. 335. *Chara*

Left, portion of a plant; right, section through apex of a long branch, showing a single-celled growing point

between highly specialized eggs and spermatozoids. In this respect it is much more advanced than *Ulothrix*, where fusion is between two ciliated gametes. Owing to the fact that the

zoöspores and spermatozoids of *Oedogonium* have a circle of cilia, and that the cells have a peculiar method of division, this genus does not seem to be closely related to such plants as *Ulothrix*.

### CHARA

**Structure.** *Chara* is a highly developed green alga which is common in fresh water. It belongs to the order *Charales*.

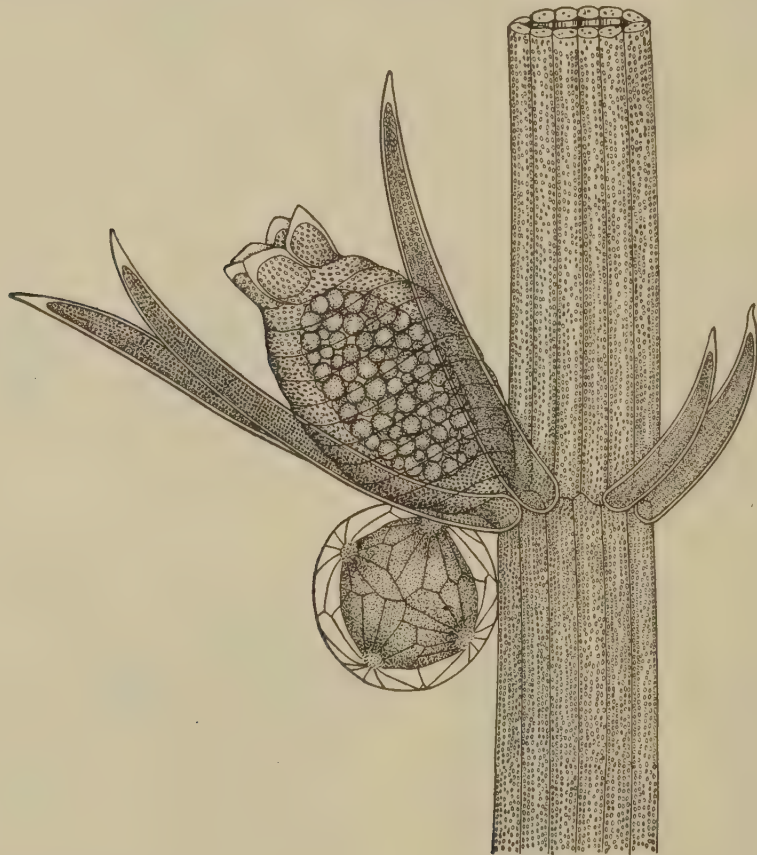


FIG. 336. A branch of *Chara* bearing a large oval oögonium; below this is a rounded antheridium. ( $\times 45$ )

The vegetative portion of *Chara* consists of a much-branched thallus (Fig. 335) which is anchored to the substratum by branched filaments known as rhizoids. The growth in length of *Chara* is due to a single apical cell (Fig. 335). The branches are of two kinds: long ones of indeterminate growth and short ones of limited growth. The long branches consist of long internodes and short nodes. The internode is composed of a large cell surrounded by a single layer of smaller cells called cortical



cells. At the nodes there are whorls of short branches of limited growth. These short branches bear still shorter branches and the sexual organs (Figs. 335, 336).

**Reproduction.** No asexual reproduction by spores is known in *Chara*. Sexual reproduction results from the fertilization of eggs by spermatozoids. The

oögonium is egg-shaped and consists of a single egg surrounded by a flasklike jacket of spirally wound cells (Fig. 336). The egg is very large and contains numerous starch grains. The antheridium is spherical, is red when mature, and has an exceedingly complex structure (Fig. 336).

There is an outer layer consisting of eight cells known as *shield cells*. From each of these there projects inward a long cell, the *manubrium* (Fig. 337), at the end of which is a rounded cell, the head cell. The head cells produce varied numbers of small cells. From each

of the ultimate cells there grow two long filaments, each of which contains about two hundred cells. A spermatozoid is developed in each of these (Fig. 337). When an antheridium is mature, it is ruptured and the spermatozoids escape and swim around and enter the necks of the oögonia. A single sperm cell fuses with an egg cell to form an oöspore. When an oöspore germinates, it grows into a new *Chara* plant (Fig. 338).

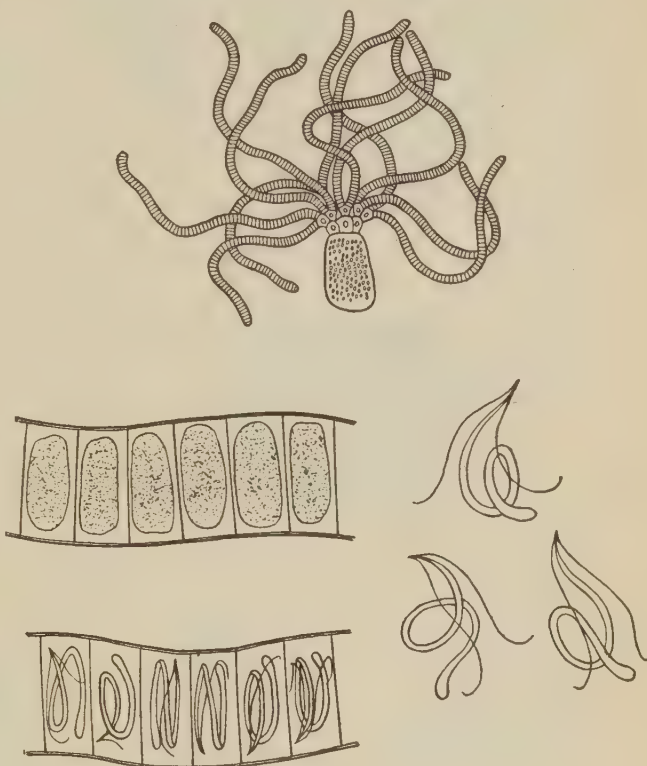


FIG. 337. *Chara*

Above: a manubrium with head and ultimate cells and filaments of sperm cells. Below: at the left, portions of two filaments, one showing cells before formation of spermatozoids, the other with contents transformed into spermatozoids; at the right, mature spermatozoids.

(× 1000)

**Relationship.** The *Charales* are generally considered as having been derived from green algæ, but they are so very different from the remainder of the green algæ that they are frequently, if not usually, placed in a separate class.

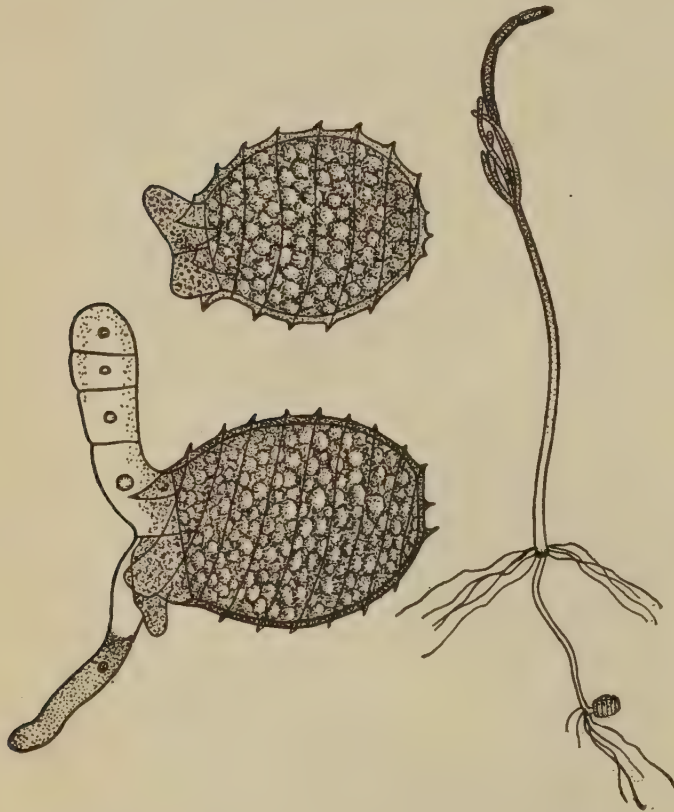


FIG. 338. Stages in the germination of *Characeae*

The two on the left redrawn after De Bary; the one on the right redrawn after Pringsheim

*Vaucheria* is found in water and in damp places. A plant consists of a sparingly branched filament, in the vegetative portion of which there are no cross walls. The cell wall is lined with protoplasm, while a vacuole extends through the center of the filaments. Numerous nuclei and chloroplastids occur in the protoplasm. The plant is attached to the substratum by a colorless branched filament, the holdfast.

**Reproduction.** *Vaucheria* reproduces asexually by the production of compound zoöspores. The end of a filament enlarges and is cut off from the remainder by a cell wall. The contents are then transformed into a large oval zoöspore (Fig. 340). This contains many nuclei and has numerous cilia, which occur in pairs, each pair being opposite a nucleus. Since each pair of

### VAUCHERIA

**Structure.** *Vaucheria* is a representative of the order *Siphonales*, which is characterized by the fact that the vegetative (nonreproductive) portion of the plant consists of branching filaments with many nuclei but no cross walls. Cross walls normally occur only in connection with the reproductive organs.

*Vaucheria* is found in water and in damp places. A plant consists of a sparingly branched filament, in the vegetative



cilia occurs in connection with a nucleus, the zoöspore is regarded as a compound structure composed of many uninuclear, biciliated zoöspores. The zoöspore with the surrounding wall

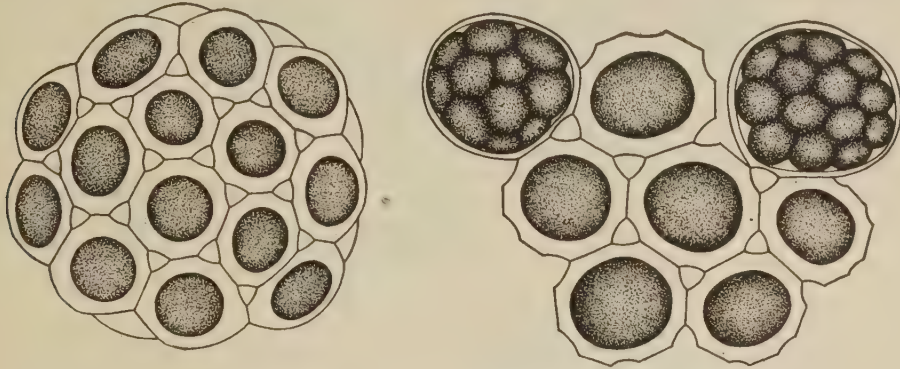


FIG. 339. *Cellastrum*, a colonial nonmotile green alga

Left, colony; right, portion of a colony, two cells of which are giving rise to daughter colonies. ( $\times 750$ )

is known as a zoösporangium. The zoöspore escapes by the rupture of the wall of the zoösporangium. After swimming about for a while the zoöspore comes to rest, develops a cellulose wall, and grows into a new plant (Fig. 341). In this process the zoöspore produces two tubular filaments, one of which develops a holdfast by which the plant becomes attached to the substratum.

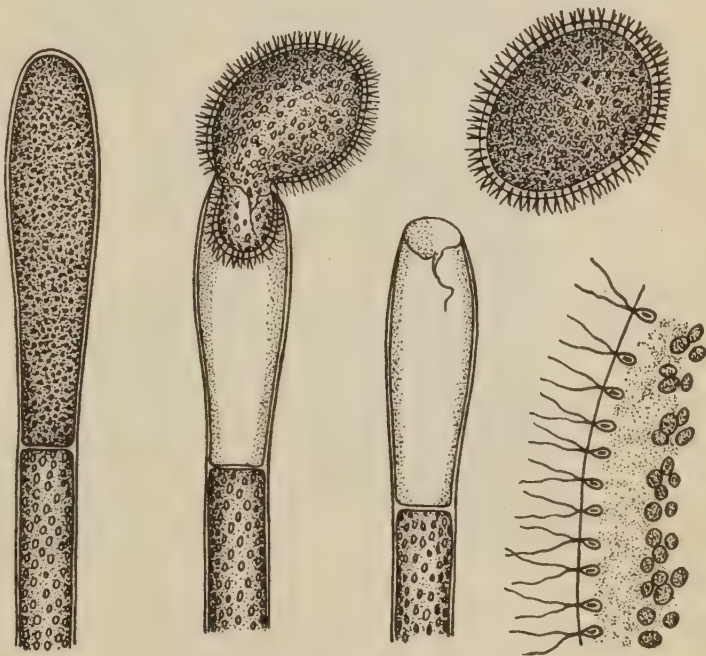


FIG. 340. *Vaucheria*

Sexual reproduction is by means of eggs and spermatozooids. The eggs occur singly in oögonia,

First three figures, formation and escape of zoöspore; fourth figure, section of a portion of zoöspore, showing two cilia opposite each nucleus. (The first three figures redrawn after Goetz from Oltmanns; the last figure redrawn after Strasburger from Oltmanns)



FIG. 341. Germination of zoospore of *Vaucheria*  
Redrawn after Sachs from Oltmanns

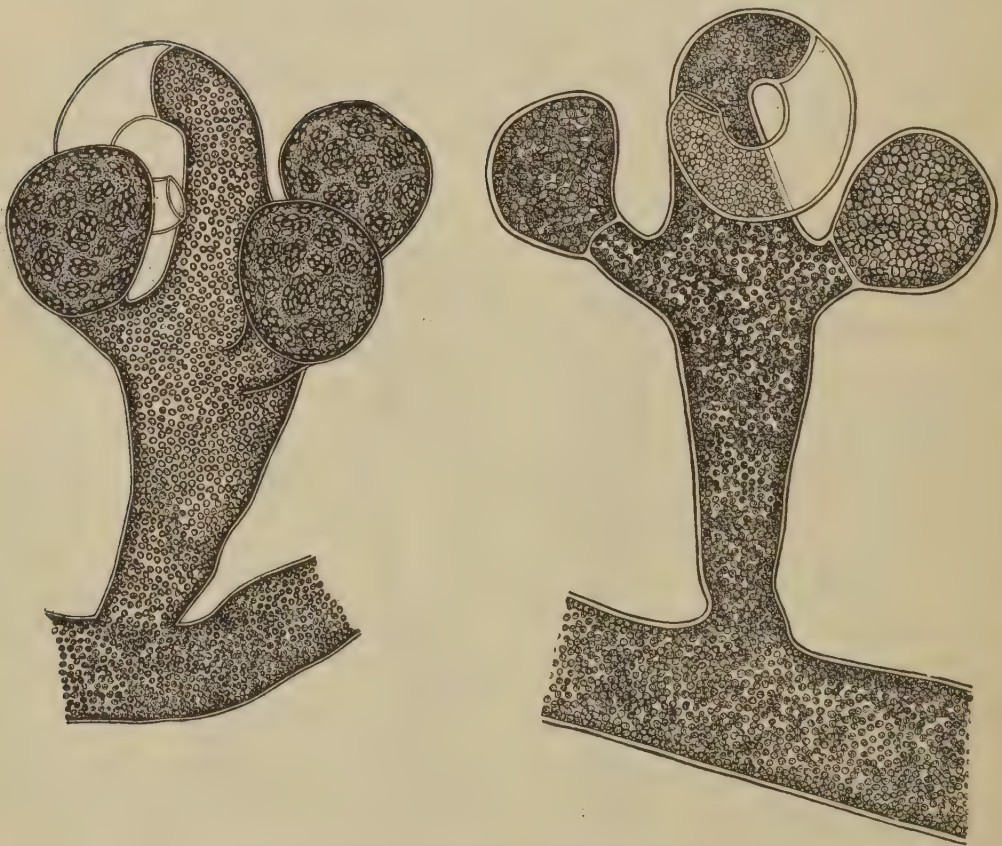


FIG. 342. Branches of *Vaucheria*  
Left, branch with three oögonia and empty antheridium; right, branch with two oögonia and empty antheridium. ( $\times 185$ )



while the sperms are produced in considerable numbers in antheridia (Fig. 342). The oögonia and antheridia are either developed directly from the vegetative filament (Fig. 343) or occur on special short branches (Fig. 342). The oögonium is a large, round structure, usually with a projection, or beak, and is cut off by a wall. It contains a single egg, which when mature has only one nucleus. The antheridium is a small, tubular branch which is usually curved at the time of maturity. The antheridium is cut off from the vegetative filament by a cross wall. When the egg is mature, the oögonium opens at the beak. The mature antheridia also open and in this way allow the sperms to escape. These swim around and some reach an oögonium, where one of them fuses with an egg. The fertilized

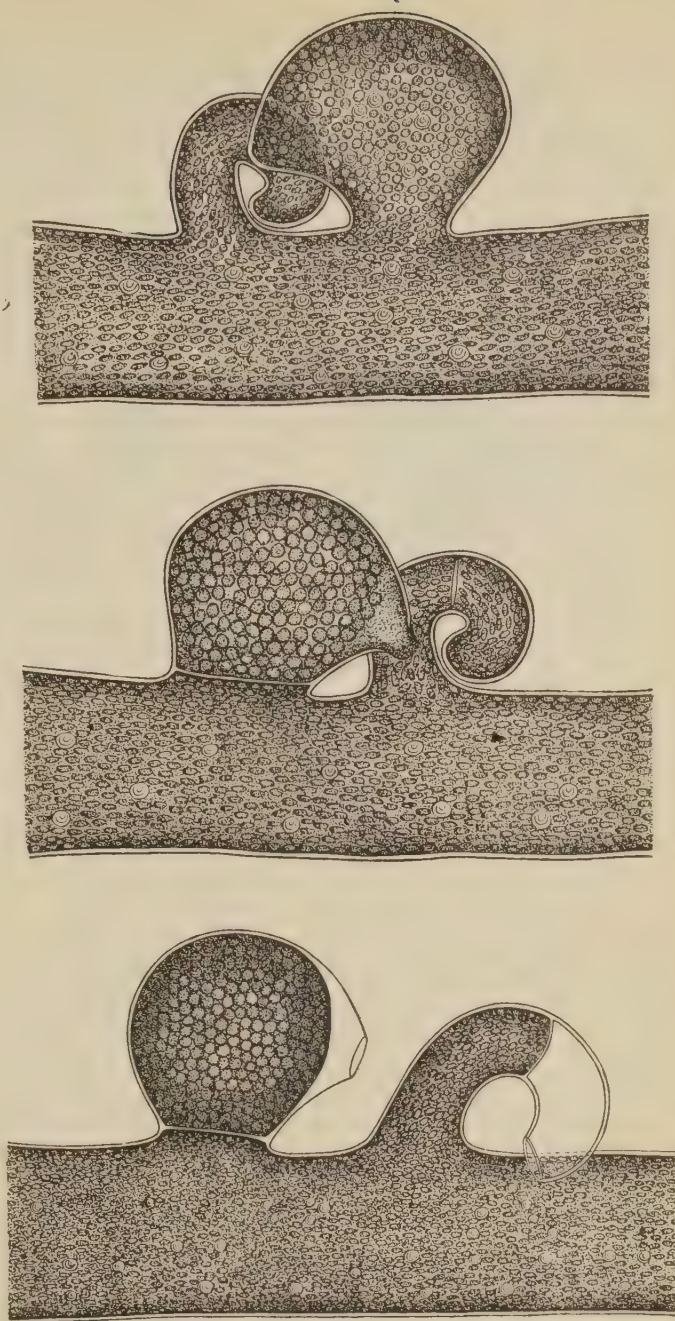


FIG. 343. Vegetative filaments of *Vaucheria* bearing antheridia and oögonia

First figure, antheridium and oögonium not separated from filament; second figure, oögonium and antheridium separated by cross walls; third figure, antheridium after discharge of spermatozoids, egg fertilized. ( $\times 145$ )

oögonium, where one of them fuses with an egg. The fertilized

egg surrounds itself with a thick wall and becomes a resting spore. After a period of rest it develops directly into a new plant.



FIG. 344. *Halimeda opuntia*, a calcareous green alga

**Relationship.** The *Siphonales*, the order to which *Vaucheria* belongs, are a branch of the *Chlorophyceae* which is the result of a line of evolution very different from the main line that gave rise to higher green plants. Since we regard flowering plants as a culmination of the evolutionary process in plants, the order *Siphonales* represents a side branch of evolution. One of the subclasses of fungi is believed to have been derived from this order.

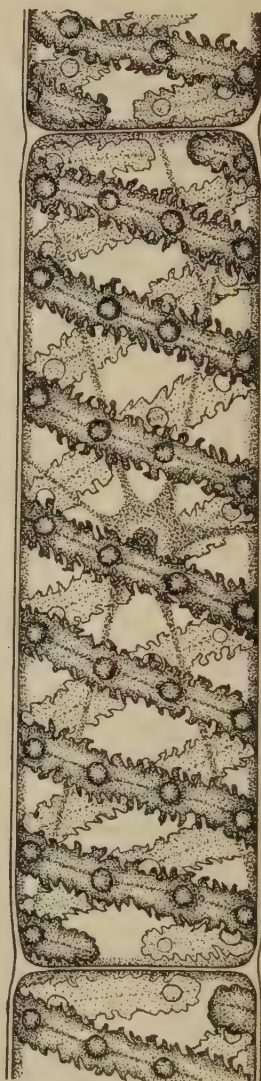


FIG. 345. A cell of *Spirogyra*. ( $\times 425$ )

### SPIROGYRA

**Cell structure.** *Spirogyra* is a filament composed of cells joined end to end, all of the cells being similar in structure. Each cell contains one or more chloroplastids which have the form of spiral bands (Fig. 345). In each chloroplastid there is a longitudinal



row of conspicuous pyrenoids. A single nucleus is in the center of the cell and is frequently conspicuous. The nucleus is surrounded by cytoplasm, and cytoplasm also lines the cell wall and extends as fine strands from the cytoplasm around the nucleus to the peripheral cytoplasm. The cells of *Spirogyra* are alike not only in structure but also in function. Each cell performs all the vegetative functions of the plant. Every cell absorbs

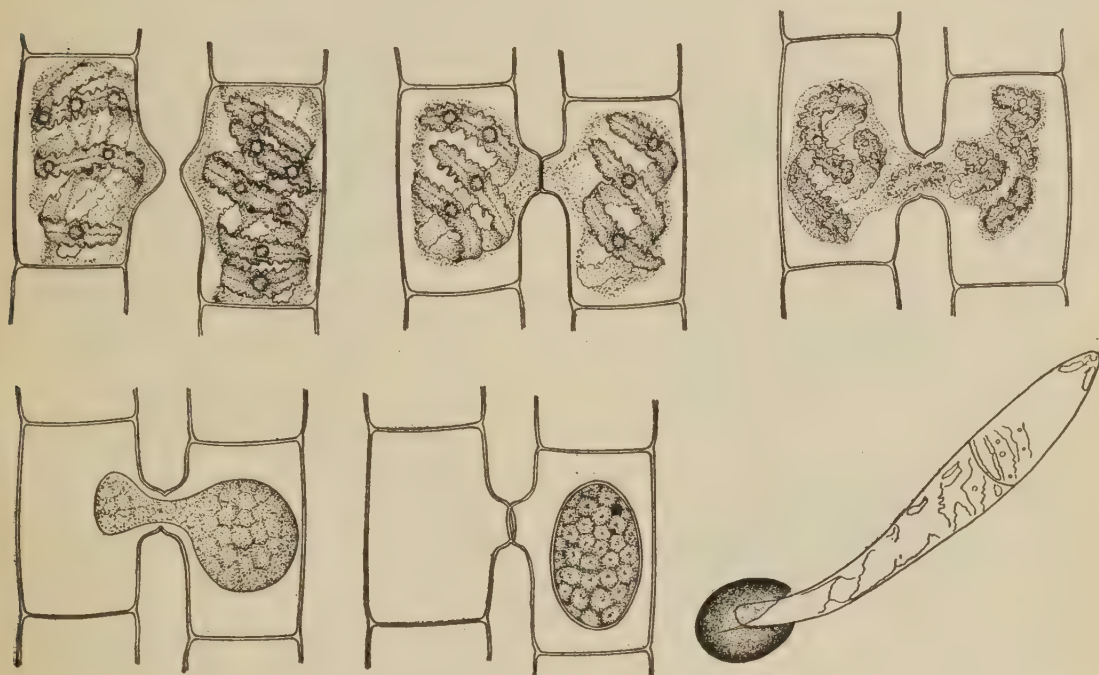


FIG. 346. *Spirogyra*

Successive stages in conjugation and formation of zygospore ( $\times 165$ ) and germination of zygospore

water, carbon dioxide, and mineral matter; every cell carries on photosynthesis; and every cell has the power of growing and dividing. A filament grows by the division of its cells and the subsequent elongation of the daughter cells. One filament may break into two and thus form two filaments.

**Reproduction.** *Spirogyra* reproduces sexually by conjugation, which is the union of two similar or nearly similar cells to form a zygospore. In most species this process is initiated by two filaments coming to lie side by side. Projections then grow singly from the cells of each filament toward those of the opposite

filament (Fig. 346). When the projections from opposite cells come into contact, the walls between them are absorbed so that a tube connects a cell of one filament with a cell of the opposite

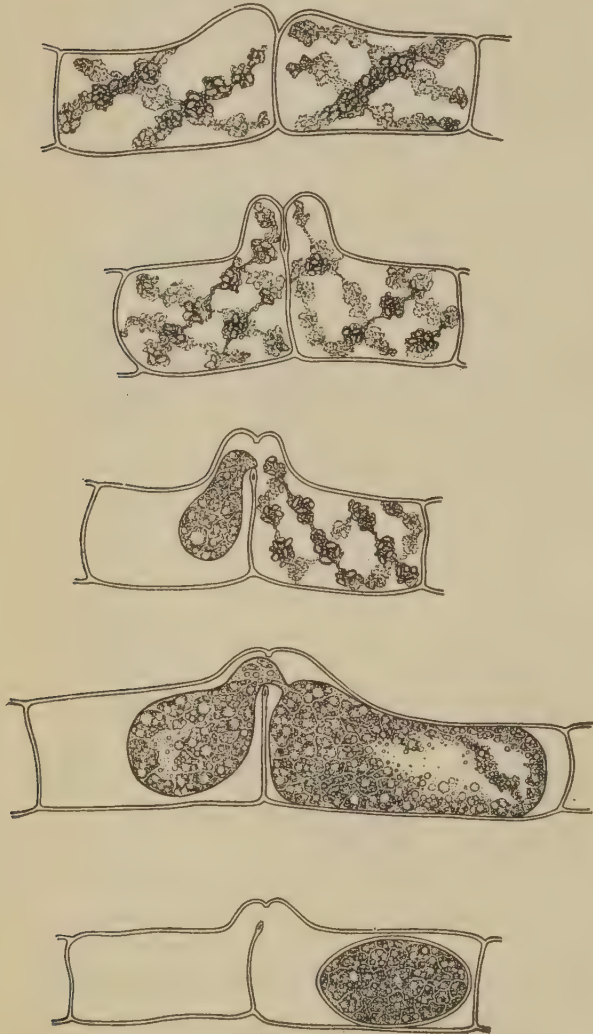


FIG. 347. Conjugation of *Spirogyra*

Successive stages in conjugation in a species in which conjugation is between two neighboring cells; the last figure shows mature zygospore. ( $\times 200$ )

for instance, the ordinary vegetative cells of *Spirogyra* would be killed quickly by drying, but the zygospores can withstand prolonged periods of drying. In consequence of this fact they can be transported from one body of water to another, or, when the water in a pool dries up, they can survive until they are again surrounded by water.

filament. The protoplasm of one cell then moves through the tube into the opposite cell and fuses with the protoplasm of that cell. Usually all the cells of a filament behave alike in sexual fusion; for example, if one cell of a filament retains its contents and receives the protoplasm from the opposite cell, all cells in the same filament do likewise.

If the filaments having only receiving cells can be considered as indicating a female condition, *Spirogyra* shows what may be regarded as a very slight differentiation of sexes.

The fusion of the protoplasm of two cells results in the formation of a zygospore, which surrounds itself with a thick cell wall (Fig. 346). The zygospores can withstand adverse conditions:



In some species the zygospore is formed by the conjugation of two adjacent cells in the same filament (Fig. 347). In such cases projections grow from the adjacent ends of the two cells. When the projections meet, the walls are absorbed, so that the two cells are connected by a tube, through which the protoplasm from one cell enters the other.

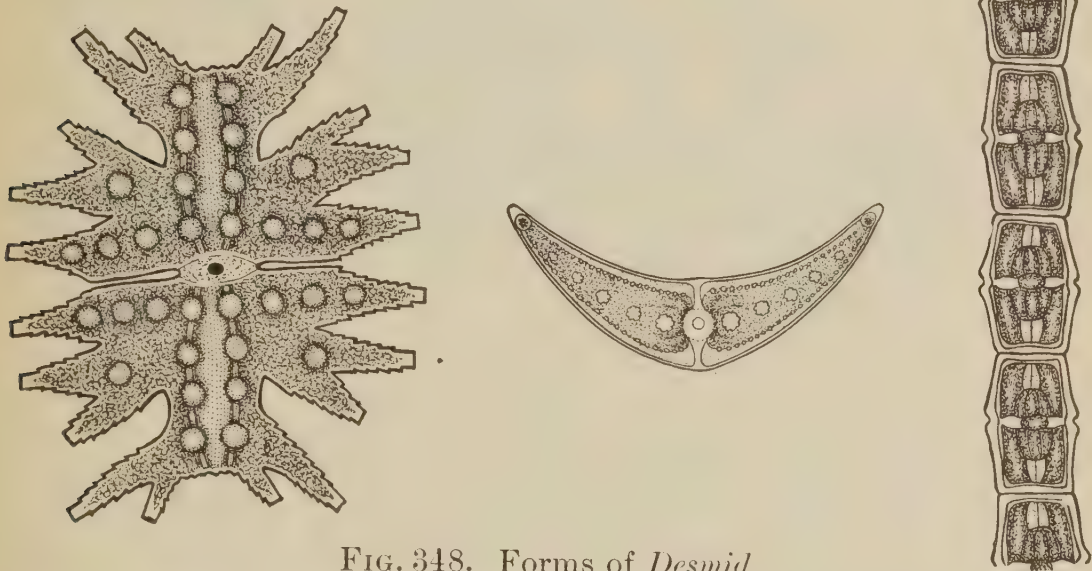


FIG. 348. Forms of *Desmid*

Desmids are either single cells or cells joined together in filaments. They are related to *Spirogyra*. See Fig. 349. ( $\times 220$ )

**Relationship.** *Spirogyra* belongs to the order *Conjugatae*, which is characterized by the absence of ciliated gametes and zoöspores. In all members of the order sexual reproduction is due, as in *Spirogyra*, to the conjugation of two similar or nearly similar cells. The order is a branch of the *Chlorophyceae*, and although the members do not possess ciliated cells, they were probably derived from plants which did have such cells. As the line of evolution shown by the *Conjugatae* appears to end with the order, it is regarded as a side branch of the evolutionary process in plants.

#### CLASS PHAEOPHYCEAE (BROWN ALGÆ)

The *Phaeophyceae* are multicellular algæ having a brown color, and for this reason they are called brown algæ. The motile reproductive cells have two cilia, which are inserted on the side of a cell, instead of at the anterior end as in the *Chlorophyceae*. Like

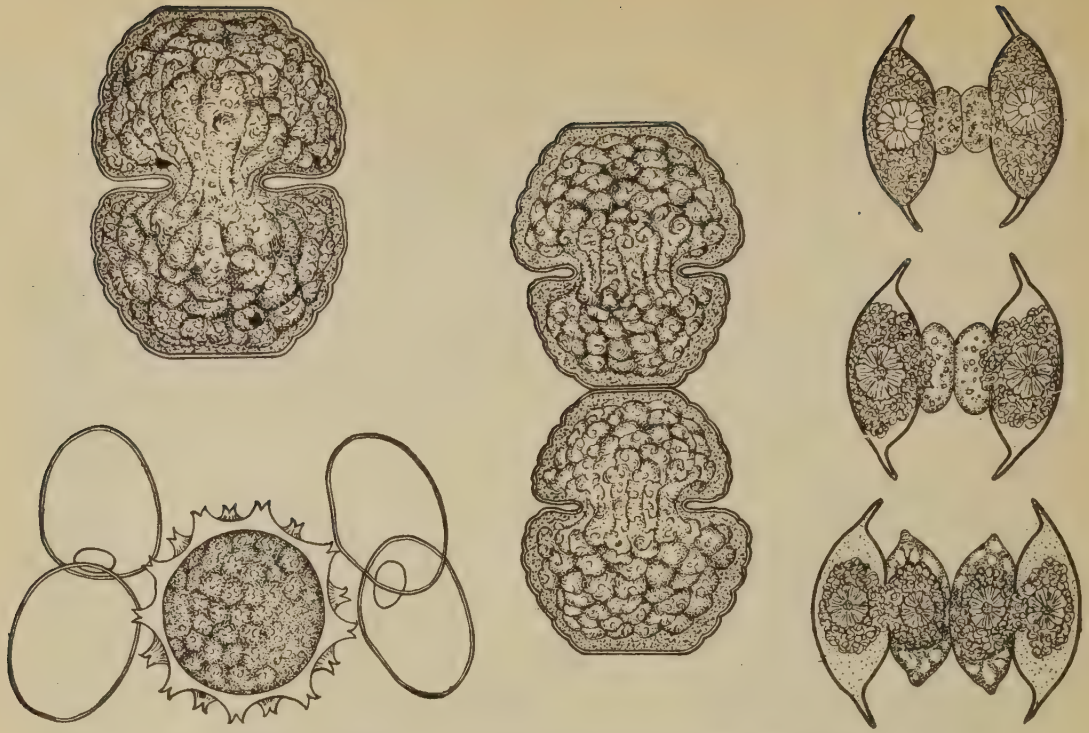


FIG. 349. *Cosmarium* and *Anthrodesmus*

Desmids reproduce sexually by the conjugation of two cells (the walls of each separate into two parts; the contents escape and fuse to form a zygospore, which surrounds itself with a thick wall); asexually by division of one cell into two across the narrow part or isthmus, each half growing out a new half. Left: above, mature individual of *Cosmarium* ( $\times 1150$ ); below, a zygospore ( $\times 700$ ). Center: a stage in asexual reproduction of *Cosmarium*. Right: three successive stages in asexual reproduction of *Anthrodesmus* ( $\times 1090$ ). See Fig. 348

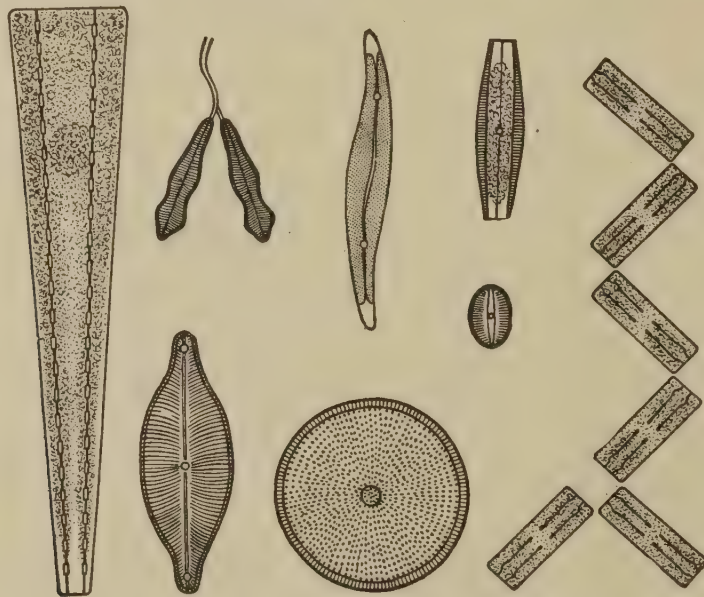


FIG. 350. Forms of diatoms

Diatoms are algæ which are brown and have siliceous shells. Reproduction is similar to that of desmids (see Figs. 348 and 349). Diatoms are very abundant in both fresh and salt water. Many cleansing preparations owe their efficacy to the scouring action of the siliceous shells of diatoms. ( $\times 225$ )



the *Chlorophyceae*, the *Phaeophyceae* show a great variety of forms (Figs. 351–353) and various degrees of sexual differentiation. The *Phaeophyceae* are found mostly in salt water. They

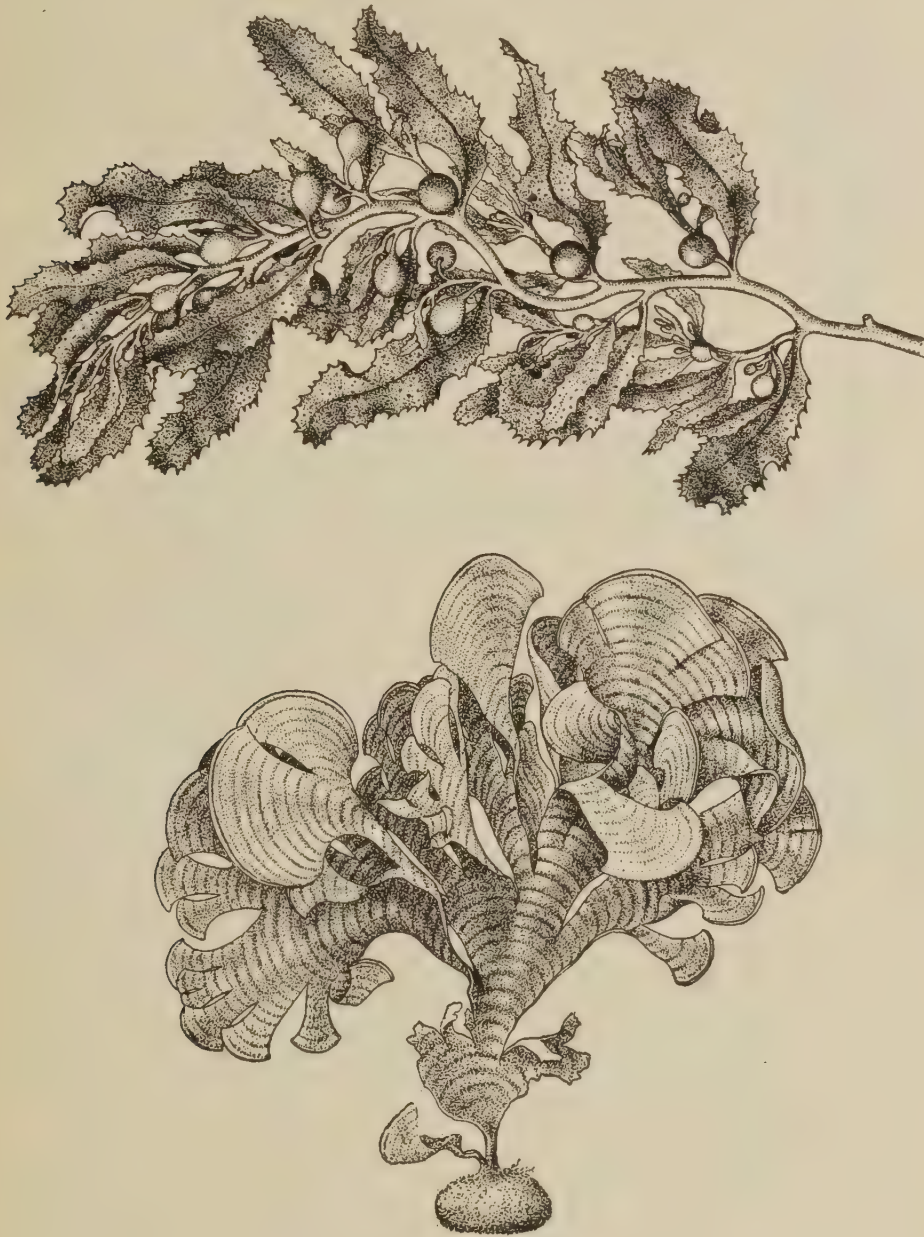


FIG. 351. Brown algæ

Above, *Sargassum* ( $\times \frac{3}{4}$ ); note that the plant is divided into stemlike and leaf-like portions and also has rounded air bladders which contain air and add to the buoyancy of the plant. Below, *Padina australis* ( $\times \frac{2}{3}$ )

include the largest and some of the most conspicuous seaweeds. A simple form is *Ectocarpus*, in which the vegetative body consists of branched filaments composed of single rows of cells

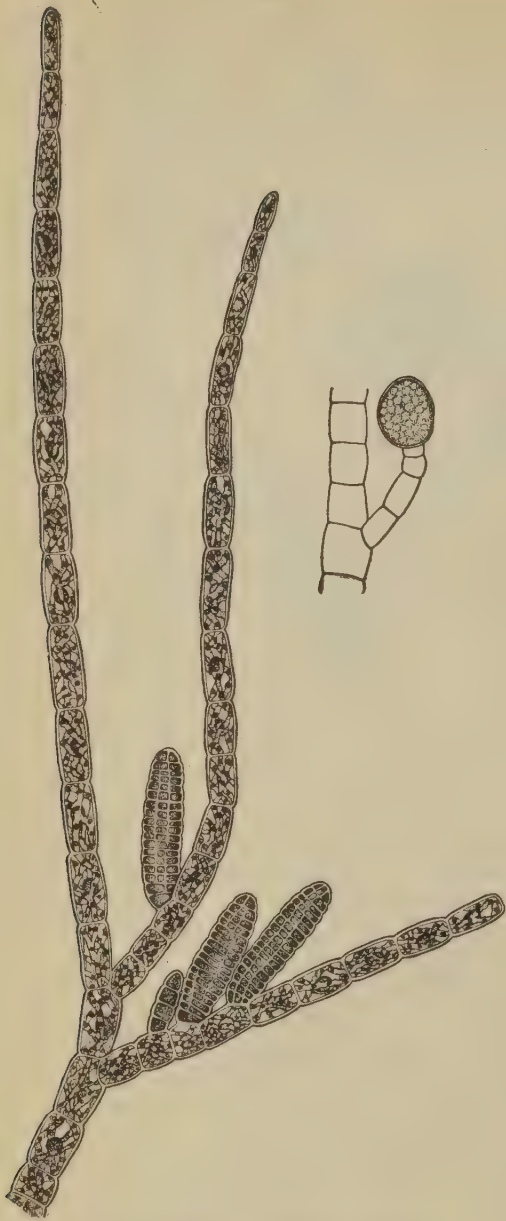


FIG. 352. *Ectocarpus*

This is a filamentous brown alga that reproduces sexually by the formation of a large number of gametes in gametangia, shown in the drawing to the left as oval structures. *Ectocarpus* reproduces asexually by zoöspores formed singly in zoösporangia, as shown in the drawing at the right. ( $\times 145$ )

(Fig. 352). Asexual reproduction is by means of zoöspores which are produced singly in zoösporangia (Fig. 352). Sexual reproduction is due to gametes which are formed in large numbers in gametangia (Fig. 352). All the gametes are similar in appearance.

*Fucus* (Fig. 353) and *Sargassum* (Fig. 351), of the order *Fucales*, are well-known examples of more complex brown algæ. *Sargassum* is sometimes found floating in the sea in large quantities. A large tract of the Atlantic Ocean is known as the Sargasso Sea on account of the *Sargassum* floating there. The *Fucales* have no asexual method of reproduction but reproduce sexually by the fertilization of eggs by spermatozoids. The oögonia and antheridia are borne in flask-shaped depressions called conceptacles (Fig. 353).

#### CLASS RHODOPHYCEAE (RED ALGÆ)

The *Rhodophyceae* are usually red or violet or sometimes dark purple or reddish brown. The color is due to a red pigment, phycoerythrin, which masks the chlorophyll. The red algæ are mostly

marine forms and include the majority of seaweeds. They are frequently abundant along the coasts and are often objects of great beauty. The *Rhodophyceae*, like the *Phaeophyceae* and the



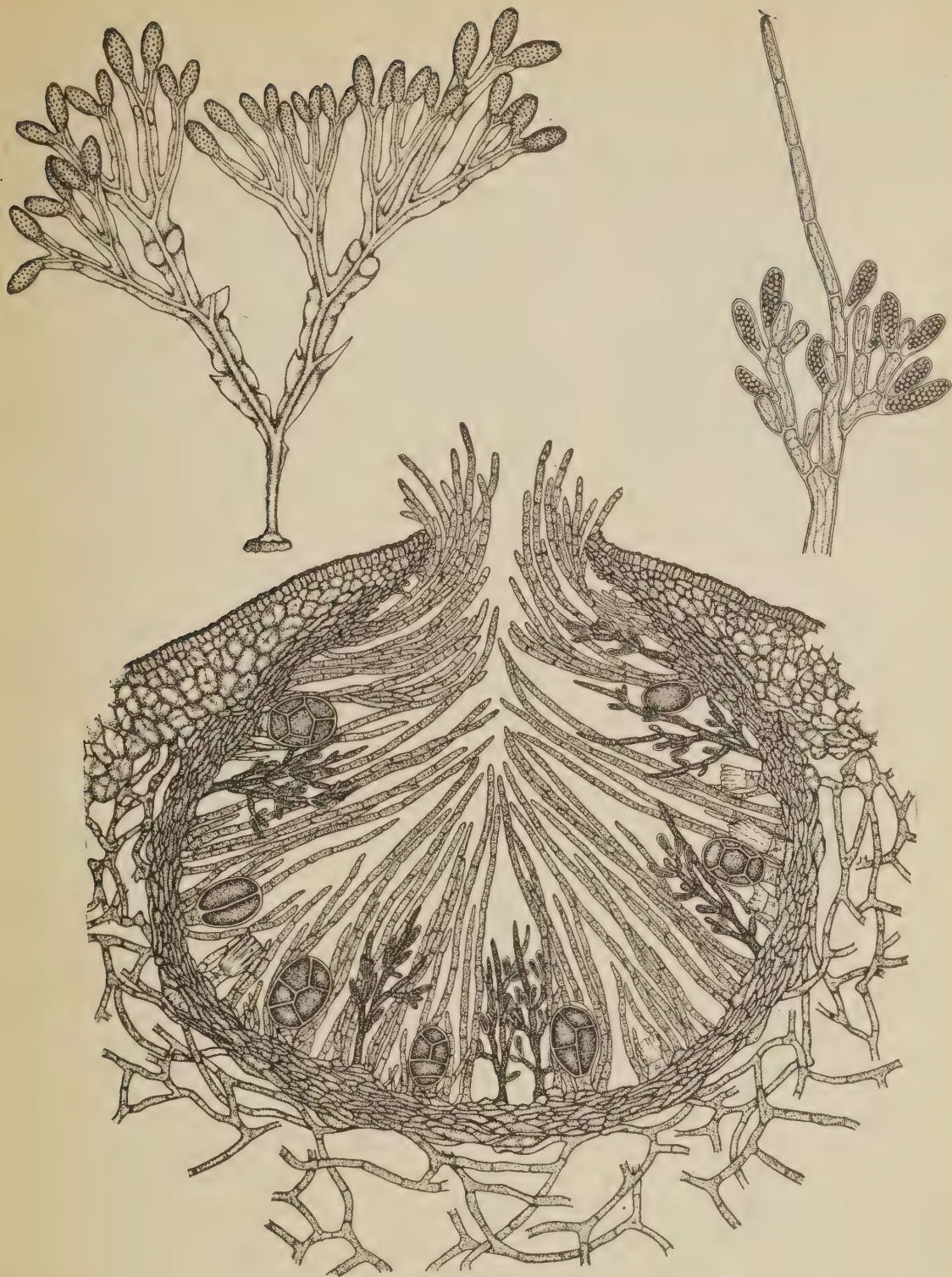


FIG. 353. *Fucus*, a brown alga

Upper left, complete plant, showing holdfast attached to rock and expanded fertile tips of the thallus ( $\times \frac{1}{4}$ ). The dots in the fertile tips are openings into flask-shaped conceptacles containing gametes. The gametes are eggs and spermatozooids, and are found in the same conceptacles or on different plants, depending on the species. Below, section of conceptacle showing branched antheridial filaments and oval oögonia, each of which when mature contains eight eggs ( $\times 65$ ). Upper right, antheridial filament with numerous antheridia, each of which contains many spermatozooids ( $\times 160$ )

*Chlorophyceae*, exhibit a great variety of forms (Fig. 354). Reproduction is either by asexual spores or by the fertilization of female cells by male cells (Fig. 355). Unlike the male cells

of other algæ, those of the *Rhodophyceae* are not motile but are transported by the movement of the water.

**Economic importance of algæ.** The direct economic importance of algæ is comparatively slight. Some of the seaweeds are used as food in various countries, the collection of them for food being an important industry in Japan. The larger brown algæ serve as sources of potash and iodine. Agar, used as a medium for growing bacteria and also as a medicine, is obtained from red algæ. Certain of the brown and red algæ are used



FIG. 354. Red algæ

Upper left, *Chondrus crispus*; upper right, *Porphyra*; lower left, *Polysiphonia violacea*; lower right, *Corallopsis salicornia*

as medicine. Fossil diatom shells (Fig. 350) are the basis of many cleansing preparations which cleanse by their scouring action, while dynamite is nitroglycerin absorbed in diatomaceous earth. Although the direct importance of algæ is not great, they are indirectly of tremendous value as the ultimate source of the food of fishes.



CLASS FUNGI

The *fungi* are saprophytic or parasitic plants which are related to the algæ but which do not possess chlorophyll. They are frequently colorless, but may have various colors and may even be green, although their color is never due to chlorophyll. The plant body consists of a system of threads (*hyphæ*) which are single rows of cells. A mass of *hyphæ* is known as a *mycelium*. The mycelium may be either a loose, cobwebby structure, as in molds (Fig. 359); relatively hard and firm, as in mushrooms (Fig. 381); or even woody, as in the bracket fungi (Figs. 382, 383). In no case, however, do fungi produce true tissues, as the plant body of even the woody forms is made up of interlacing *hyphæ*, and the *hyphæ* are always single rows of cells.



FIG. 355. Sexual reproduction in *Nemalion*, a red alga

In the first drawing, the long branch at the left bears numerous antheridia, whereas the one at the right terminates with a special kind of oögonium known as a carpogonium. Two male cells from the antheridia are in contact with the projection from the carpogonium. A male cell will fuse with the projection from the carpogonium, and its contents will pass into the carpogonium. The second and third drawings represent stages in formation of spores from the carpogonium.

(Redrawn after Bonnet and Thuret)

Reproduction in the fungi is by means of spores, which may be formed either asexually or as a result of sexual fusion.

Many plants besides the fungi lack chlorophyll and live as saprophytes or parasites. Among these are the bacteria. The fungi can easily be distinguished from the bacteria by their larger size and more complex structure. Like the algæ, and unlike the

bacteria, they have definite and highly organized nuclei. Many flowering plants lack chlorophyll and live as saprophytes or parasites. These can be distinguished from the fungi by their structure, as the flowering plants produce true tissues, have flowers, and do not reproduce by means of spores. Many algæ are composed of single rows of cells and reproduce by spores, but they possess chlorophyll. From the foregoing it will be seen that the fungi can be distinguished by the following three characters: the vegetative body is a mycelium, they lack chlorophyll, and they reproduce by spores.



FIG. 356. Mycelium of *Saprolegnia* on an insect.  
( $\times 2\frac{1}{2}$ )

The fungi exhibit a great diversity of forms and structures. They are divided into three subclasses: the *Phycomycetes*, the *Ascomycetes*, and the *Basidiomycetes*.

There are many fungi whose systematic position is uncertain, and these are placed together in a group called *Fungi Imperfecti*.

#### SUBCLASS *PHYCOMYCETES*

This group can be distinguished from other fungi by the fact that cross walls are not found in the hyphæ except when reproductive cells are produced. *Phycomycetes* are divided into two orders: *Oömycetes*, reproduced sexually by means of oögonia and antheridia, and *Zygomycetes*, reproduced sexually by the fusion of two similar filaments.

***Saprolegnia*. Structure.** The *Oömycetes* are characterized by the fact that sexual reproduction is by the fertilization of eggs. In order to get an idea of this order we may consider a typical example, the genus *Saprolegnia*. This genus (Fig. 356) grows abundantly in water on decaying animal and vegetable matter, and sometimes on living animals. It is frequently very destructive to fish eggs and young fishes. The vegetative part of the plant consists of a branching system of filaments without cross



walls. Some of these filaments enter the animal on which the plant is growing and absorb nutriment, while others radiate out in the water and produce reproductive structures.

**Reproduction.** *Saprolegnia* reproduces asexually by the formation of zoöspores with two cilia. These are produced in *zoösporangia* which are formed from the ends of club-shaped filaments (Fig. 357). The terminal portion of the filament is cut off by a cell wall, thus forming a zoösporangium, and the contents divide and round up to form zoöspores. These escape through an opening at the tip of the sporangium. Under favorable circumstances they finally grow into new plants.

Sexual reproduction is by means of oögonia and antheridia (Fig. 358). The *oögonia* are rounded structures which contain eggs and are cut off from the vegetative filaments by cross walls. The *antheridium* is a tubular branch which is cut off from the end of a hypha. It grows around an oögonium and produces branches which enter the oögonium and reach the eggs. In some cases a nucleus from an antheridium enters an egg and fertilizes it.

*Saprolegnia* shows various degrees of loss of sexuality. In some cases, as just described, the eggs are fertilized by the antheridia. In other cases there are both eggs and antheridia, but the antheridia do not fertilize the eggs, the latter developing without fertilization. In still other cases no antheridia are formed. Some of the *Oömycetes*, with a method of sexual reproduction similar to that of *Saprolegnia*, live as parasites in the leaves and stems of flowering plants.

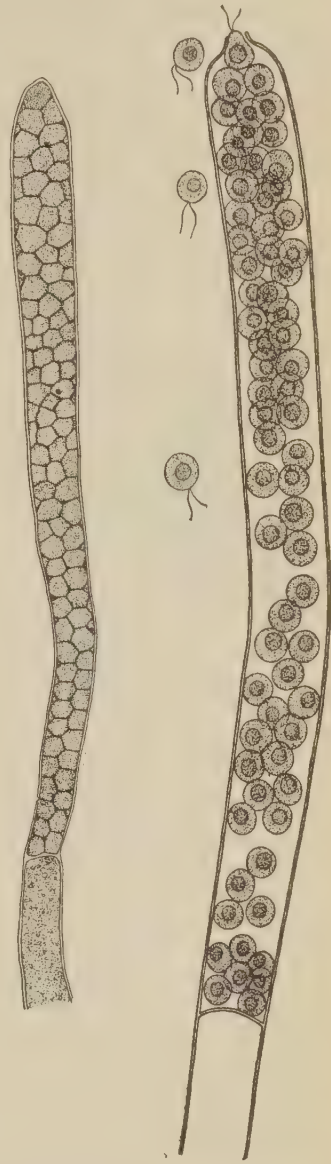


FIG. 357. Immature and mature zoösporangia of *Saprolegnia*. ( $\times 230$ )

**Relationship.** It seems very probable that the *Oömycetes* have been derived from an alga similar to *Vaucheria*. Some of the reasons for this supposition will be apparent if *Vaucheria* and *Saprolegnia* are compared. The vegetative body is very similar in the two cases, except that *Saprolegnia* lacks chlorophyll, whereas this is present in *Vaucheria*. In both cases the plant consists of branched, nonseptate filaments, that is, filaments with-



FIG. 358. Oögonia and antheridia of *Saprolegnia*. ( $\times 600$ )

out septa, or cross walls. *Vaucheria* is attached to the substratum by means of a colorless, branched filament known as a hold-fast. *Saprolegnia* is attached in a similar way, except that the filaments enter the body of the animal on which the *Saprolegnia* is growing. The zoösporangium of *Saprolegnia* has a shape similar to that of *Vaucheria*. In *Saprolegnia* there is a zoöspore for each nucleus, and each spore

has two cilia. The zoöspore of *Vaucheria* has a different structure, but we have seen that there is reason to believe that it is a compound zoöspore which can be regarded as formed by the fusion of a number of zoöspores similar to those of *Saprolegnia*, as the zoöspore of *Vaucheria* has numerous pairs of cilia, each of which is opposite a nucleus. The oögonia of the two forms are very similar, except that *Saprolegnia* usually has more than one egg, while *Vaucheria* has a single egg. The general form of the antheridia of *Saprolegnia* is likewise similar to that of the antheridia of *Vaucheria*. *Vaucheria*, however, produces sperms which swim through the water, while in *Saprolegnia* fertilization is by tubular outgrowths from the antheridia. This difference is



not important, as what are regarded as the most primitive of the *Oömycetes* have antheridia which produce sperms that swim to the oögonia, exactly as in the case of *Vaucheria*. From the above comparison it will be seen that *Vaucheria* and *Saprolegnia* have a great many points of similarity. If a holdfast of *Vaucheria*, instead of attaching itself to a rock, were to grow into the body of an animal and absorb nourishment, and if at the same time the plant were to lose its chlorophyll, we should certainly have a plant that would be very similar to some of the *Oömycetes*, such as *Saprolegnia*. We have already seen in the cases of certain flagellates that the same organism may under different conditions develop chlorophyll and manufacture its own food or lose its chlorophyll and live on organic matter. It is therefore not hard to believe that some plant similar to *Vaucheria* changed its mode of obtaining food and gave rise to the *Oömycetes*. This seems all the more likely because a number of different kinds of green plants have saprophytic or parasitic relatives.

***Rhizopus nigricans*.** The members of the order *Zygomycetes* are distinguished from those of the order *Oömycetes* by their method of sexual reproduction. In the *Zygomycetes* there are no motile cells, and sexual reproduction is due to the conjugation of two hyphæ.

*Rhizopus* is a typical example of the order *Zygomycetes*. This fungus is the white mold which grows on bread and other substances. Its distribution is world-wide, and it is exceedingly common.

**Structure.** The vegetative body consists of branching filaments. Some of these penetrate the substratum and absorb nourishment, while others extend into the air and produce reproductive bodies (Fig. 359). The vegetative hyphæ of *Rhizopus* are like those of *Saprolegnia* in being *nonseptate* and containing many nuclei.

**Reproduction.** Asexual reproduction is by the formation of large numbers of spores in spherical sporangia (Fig. 359).

Sexual reproduction is due to the conjugation of two similar filaments (Fig. 360). This takes place in the following manner:

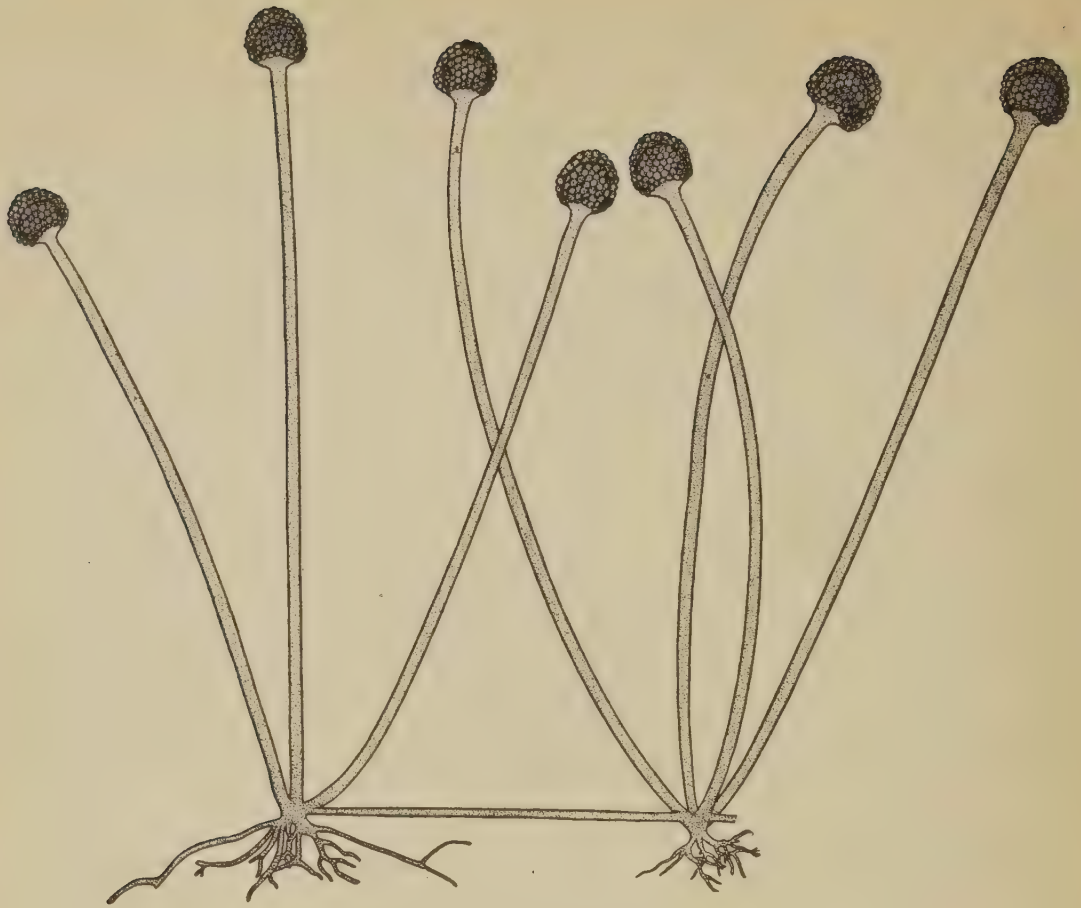


FIG. 359. *Rhizopus nigricans*

Note the absorbing hyphæ which enter the substratum and the aërial ones which project upward and bear sporangia. ( $\times 65$ )



FIG. 360. Successive stages in the conjugation and formation of zygospore in *Rhizopus nigricans*. ( $\times 80$ )



Short filaments, which are branches from neighboring hyphæ of different plants, grow toward each other, and the tips come in contact. The end of each hypha is cut off by a cross wall. This is followed by the absorption of the walls separating the two terminal cells, which fuse together to form a single cell. This grows into a rounded cell, surrounds itself with a thick cell wall, and thus becomes a resting zygospore. When the zygospore germinates, it bursts the thick wall and produces a new plant (Fig. 361).

**Relationship.** The *Zygomycetes* are generally considered as having been derived from the *Oömycetes*. In the *Oömycetes* the antheridia and oögonia are very different in size and structure, while in *Rhizopus* the conjugating hyphæ are similar. This difference is bridged to some extent by other members of the *Zygomycetes*, in which one of the conjugating filaments is much larger than the other.

If we consider the evolutionary tendencies as shown by the *Phycomycetes*, it will be evident that they have taken a very different direction from that observed in many of the algæ. The loss of chlorophyll by the *Oömycetes*, with an accompanying change in the method of obtaining food so that the plants become saprophytes and parasites, may be regarded as the initial step in a process of degeneration. In the most primitive of the *Oömycetes* sexual reproduction is due to the fertilization of highly developed eggs by motile sperms, as is also the case in the green alga *Vaucheria*. In such forms as *Saprolegnia* the male cells have lost their motility, while in such members of the *Zygomycetes* as *Rhizopus* the fusing cells



FIG. 361. Germination of zygospore of *Mucormucedo*, a mold related to *Rhizopus*

Modified after Brefeld

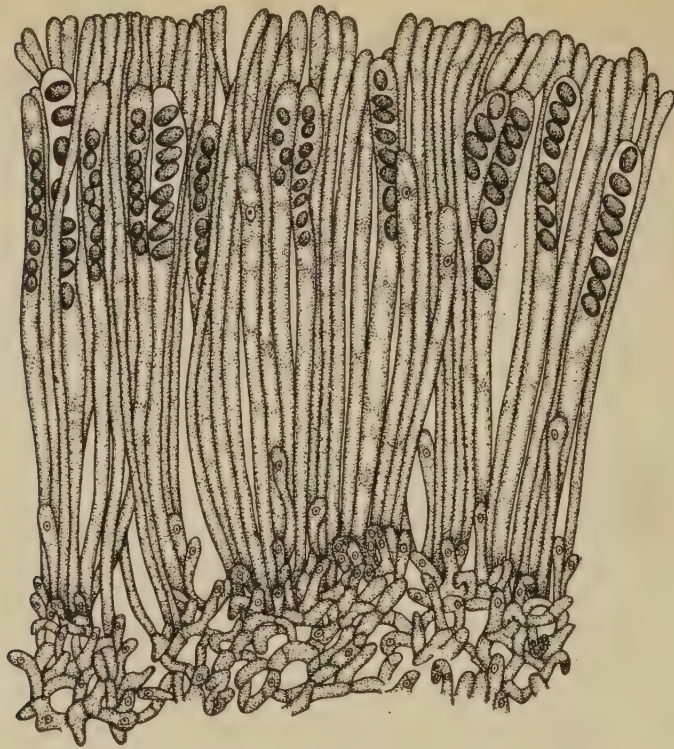


FIG. 362. Portion of hymenium of an ascomycete, *Lachnea* (see Fig. 366), showing asci in various stages of development and also paraphyses. ( $\times 200$ )



FIG. 363. Section of cuplike fruit body of *Lachnea*

Above is the hymenium composed of asci and paraphyses. ( $\times 25$ )

are entirely similar. In the evolution of many lines of algæ we see a progressive change from the fusion of similar gametes to the fertilization of eggs by sperms, whereas in the *Phycomycetes* this process appears to have been reversed.





FIG. 364. *Venturia inaequalis* (the causal organism of apple scab) on apple leaf

cylindrical structure usually containing eight ascospores (Fig. 362), but the number of spores may vary from two to many.

In a few cases the asci are borne singly, but in the vast majority of species they are produced in a layer, called the *hymenium*, which contains many asci, among which are the numerous sterile filaments, the *paraphyses* (Figs. 362, 363). In some cases the hymenium occurs as an outer covering of the fruit body, while in others

*Saprolegnia* shows a striking case of the loss of sexuality. In this genus we may find functional antheridia, antheridia which do not function, or the entire absence of antheridia.

SUBCLASS ASCOMYCETES

The *Ascomycetes* consist of fungi of various forms but characterized by having *ascospores* borne in *asci*. The *ascus* is a saclike, commonly

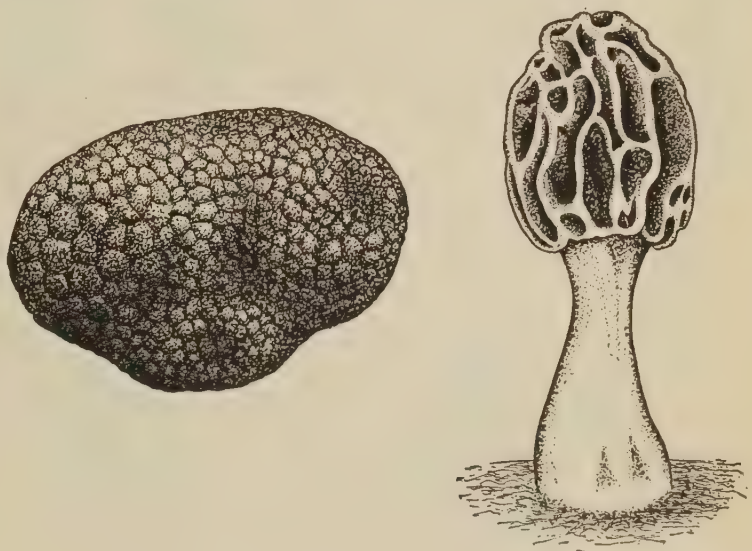


FIG. 365. Edible ascomycetes

Right, morel (*Morchella*), in which the hymenium covers the upper portion; left, truffle (*Tuber brumale*), in which the asci are inclosed within a sterile covering. ( $\times \frac{2}{3}$ )

it lines flask-shaped cavities (Fig. 364). Among the conspicuous *Ascomycetes* are the edible morel (*Morchella*) (Fig. 365) and the



FIG. 366. Fruit bodies of *Lachnea* and *Peziza*

cup-shaped forms such as *Peziza* and *Lachnea* (Figs. 363, 366). Black, charcoal-like forms are also common (Fig. 367). The edible

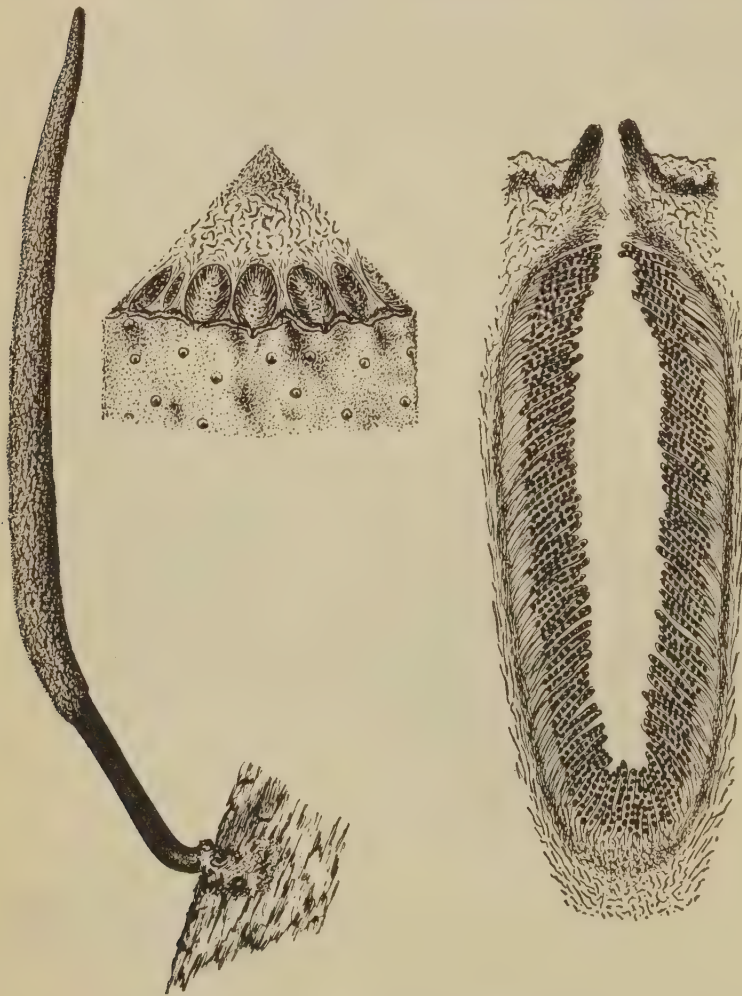


FIG. 367. *Xylaria*, an ascomycete

Left, a whole fruit body ( $\times 1$ ). Center, combined cross section and surface views of a portion of a fruit body, showing perithecia ( $\times 12$ ). Right, section of a perithecium showing hymenium; note asci in hymenium ( $\times 65$ )

truffles (Fig. 365) are tuberous *Ascomycetes* which grow underground. Many of the *Ascomycetes* are parasitic, and a large number of destructive plant diseases are produced by them (Figs. 364, 368). The yeast plant, considered in the next paragraph, is regarded as an ascomycete.

***Saccharomyces.*** The genus *Saccharomyces* contains a number of species which convert sugar into alcohol. This process is the basis of the commercial manufacture of alcohol and alcoholic drinks.



*Saccharomyces* is also used in raising bread, being sold in the form of yeast cakes. This fungus causes the sugar in the bread to be converted into alcohol and carbon dioxide, and it is the production of the carbon dioxide that is responsible for



FIG. 368. Parasitic ascomycetes

Left, *Ustilaginoidea virens*, an ascomycete parasitic on rice (*Oryza sativa*) ( $\times \frac{1}{3}$ ); right, ergot (*Claviceps purpurea*), an ascomycete parasitic on rice ( $\times \frac{2}{3}$ ). In both cases the black bodies are produced by the fungus



FIG. 369. Yeast (*Saccharomyces*), showing single cell, budding cells, and the formation of ascospores in cells. ( $\times 960$ )

the formation of holes in the bread. *Saccharomyces* is a single-celled plant. It reproduces by budding (Fig. 369). In this process a protuberance grows from the cell and becomes constricted off, thus forming a new individual.

A daughter cell may begin to bud before it has been constricted from the parent cell, and in this way chains or irregular masses of cells may be formed. Under certain conditions the contents of a cell may divide to form four spores (Fig. 369). It is on account of this method of spore formation that *Saccharomyces* is included in the *Ascomycetes*. Its relation to the *Ascomycetes* is, however, doubtful.

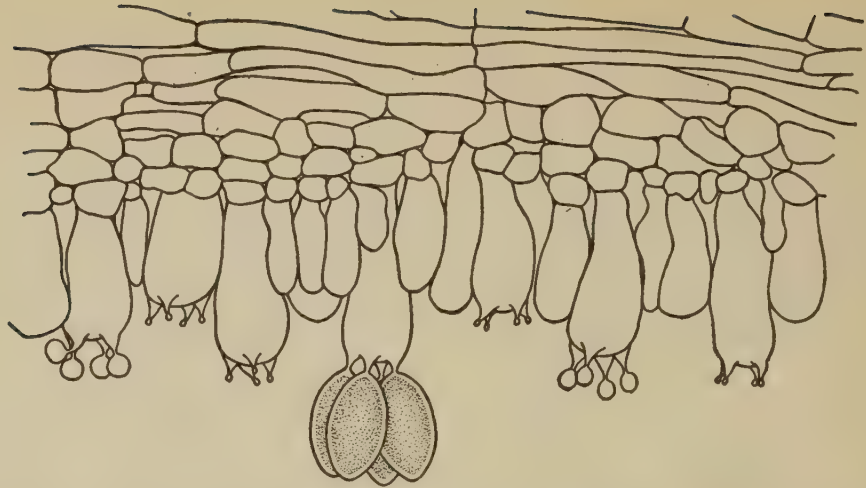


FIG. 370. °Portion of hymenium of a mushroom, showing basidia of different ages. ( $\times 860$ )

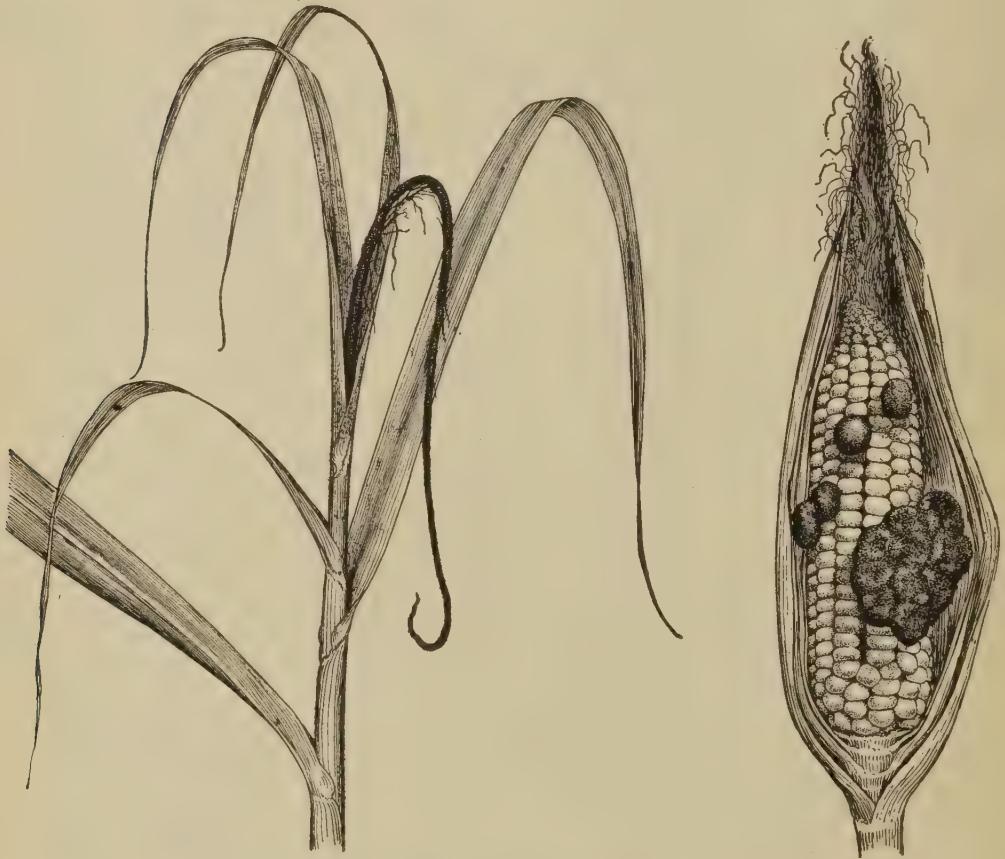


FIG. 371. The *Ustilaginales*, or smuts

Left, tip of sugar-cane plant infected by smut (*Ustilago sacchari*) ( $\times \frac{3}{20}$ ); the black whiplike tip is little more than a mass of spores. Right, ear of corn showing swellings produced by smut (*Ustilago zeae*) ( $\times \frac{3}{10}$ )



SUBCLASS *BASIDIOMYCETES*

This group is distinguished from other fungi by having spores borne on a basidium. A *basidium* is, typically, the swollen end of a hypha from which project four slender filaments (*sterigmata*), each terminating in a single *basidiospore* (Fig. 370).



FIG. 372. Spores of a smut (*Urocystis*) in tissue of onion leaf

Some *Basidiomycetes* produce other kinds of spores, as well as basidiospores. The hyphæ are like those of the *Ascomycetes* in, being septate. The largest and most conspicuous of the fungi belong to the sub-



FIG. 373. Urediniospore stage of wheat rust (*Puccinia graminis*) ( $\times \frac{1}{2}$ )

class *Basidiomycetes*. None of them live in water.

The subclass *Basidiomycetes* is divided into three sections: the *Hemibasidii*, the *Protobasidii*, and the *Eubasidii*. The *Eubasidii* are far more numerous and conspicuous than the other two sections. They are characterized by having non-septate basidii.

**Hemibasidii.** The *Hemibasidii* compose a single order, the *Ustilaginales*, or *smuts* (Fig. 371). The fungi of this order are parasitic on various plants and produce a mycelium inside the host. This mycelium develops very abundantly in certain places, and finally divides into a large number of small cells which round up and become *chlamydospores* (Fig. 372). When a chlamydospore germinates, it produces a short filament which

bears from one to twelve or more spores. The mycelium is regarded as the basidium, and the spores as basidiospores. These



FIG. 374. Aeciospore stages of rusts

Left, coffee infected with aeciospore stage of coffee rust (*Hemileia vastatrix*) ( $\times \frac{1}{3}$ ); right, aeciospore stage of wheat rust (*Puccinia graminis*) on barberry leaf ( $\times 1$ )

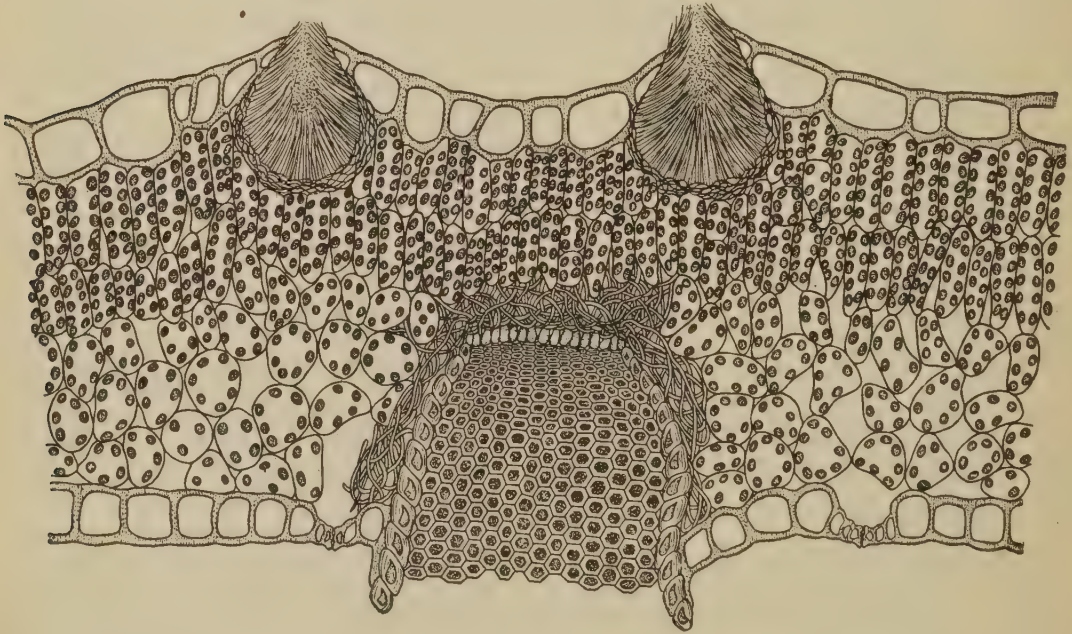


FIG. 375. Leaf infected with aeciospore stage of rust

Above are two pycnia, and below an aecium. ( $\times 165$ )

spores, on germination, produce a mycelium which infects the host. The smuts are frequently very destructive to agricultural crops. One is very conspicuous on corn, and another on sugar cane.



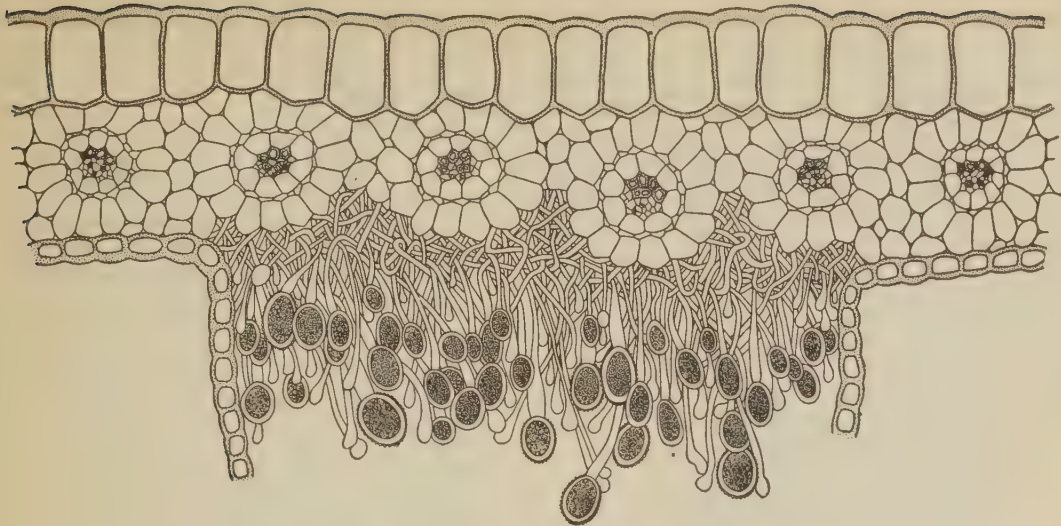


FIG. 376. Urediniospore stage of a rust

**Protobasidii.** The most important order of the *Protobasidii* is the *Uredinales*, or *rusts*, which are fungi parasitic on various green plants, and which produce some very destructive plant diseases (Figs. 373, 374). The rusts have five different kinds of spores. In some species all of these different forms are present, but in others some of them are lacking. The life history of those fungi which contain all the different kinds is as follows:

**Æciospores.** A basidiospore germinates and produces a hypha which infects the host plant, in which a mycelium is produced. Finally the mycelium produces numerous æciospores in cup-shaped structures, the *æcia* (Figs. 374, 375). The spores are formed in numerous rows. Associated with the *æcia* are flask-shaped structures, the *pycnia*, in which are found large numbers of minute *pycnospores* (Fig. 375).

The æciospores are capable of germinating at once and producing a mycelium that can infect a susceptible host. In some



FIG. 377. Teliospore stages of rusts

Left, wheat rust (*Puccinia graminis*) ( $\times \frac{1}{2}$ ); on the right, *Puccinia thwaitesii* on a dicotyledon ( $\times \frac{2}{5}$ )

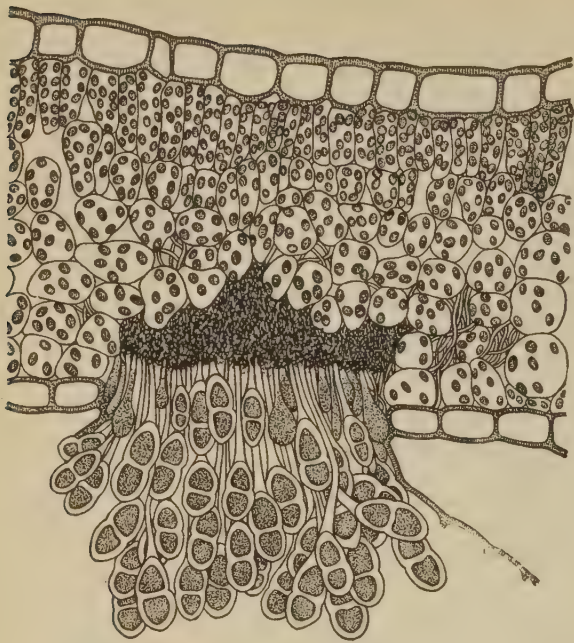


FIG. 378. Leaf infected with teliospore stage of a rust. ( $\times 140$ )

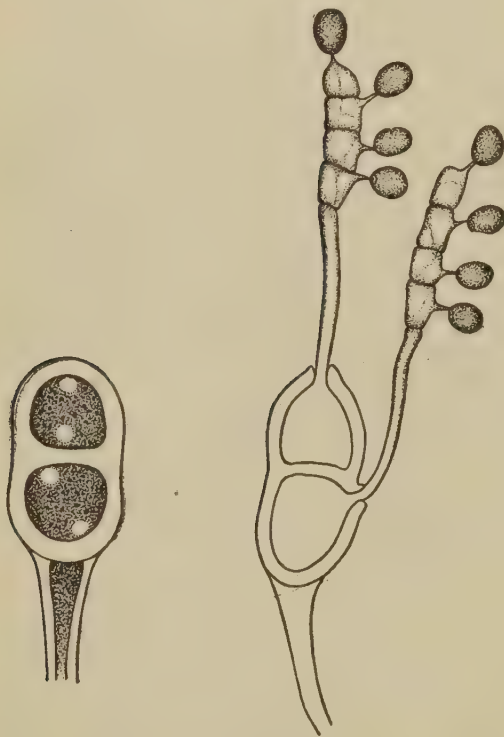


FIG. 379. Teliospore (left) and germination of teliospore (right) with production of basidiospores (somewhat diagrammatic). ( $\times 445$ )

cases the basidiospores and æciospores infect the same species, while in other cases they infect entirely different species.

**Urediniospores.** The mycelium resulting from the growth of an æciospore produces urediniospores in patches on the surface of the host. These spores are single-celled structures which occur singly at the tips of short stalks (Figs. 373, 376). A urediniospore is capable of germinating immediately and may give rise to another mycelium bearing urediniospores.

**Teliospores and basidiospores.** After the formation of urediniospores has continued for some time the mycelium may give rise to teliospores (Figs. 377, 378). The teliospores germinate by sending out short hyphæ from each cell of the spore. At the end of each hypha a row of four cells is produced, and each of these gives rise to a single basidiospore (Fig. 379).

**Life history of rusts.** In some species of the *Uredinales* all the forms of spores mentioned above are present, and they occur in the order given.



In other species one or more of the kinds of spores may be lacking. All the different forms of spores may occur on the same

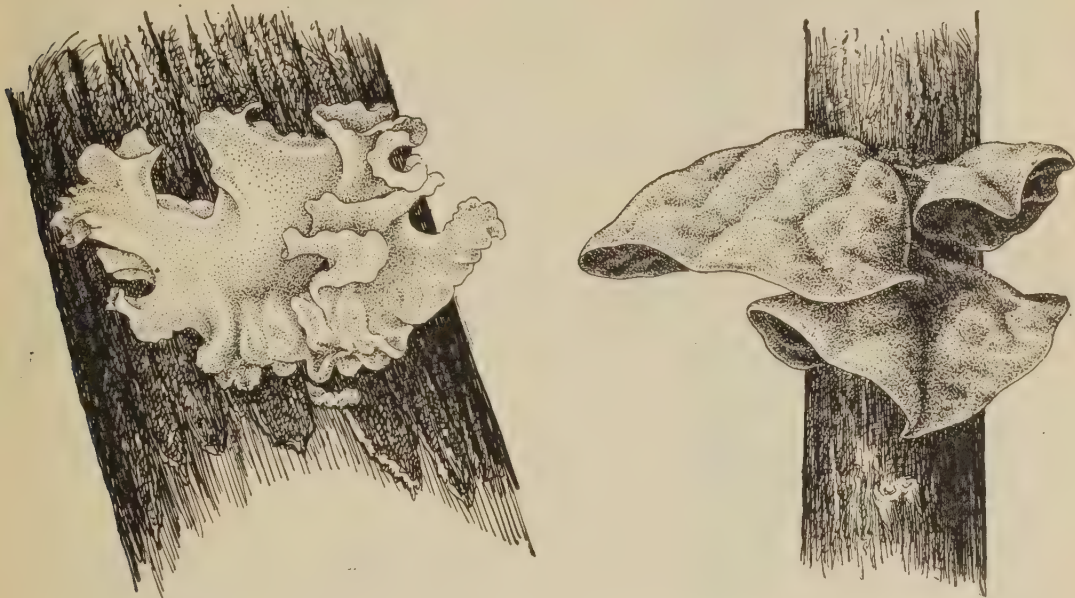


FIG. 380. *Tremella* (left) of the order *Tremellales*, and *Auricularia* (right) of the order *Auriculariales*

The orders *Uredinales*, *Auriculariales*, and *Tremellales* compose the subclass *Protobasidii*. ( $\times \frac{1}{2}$ )

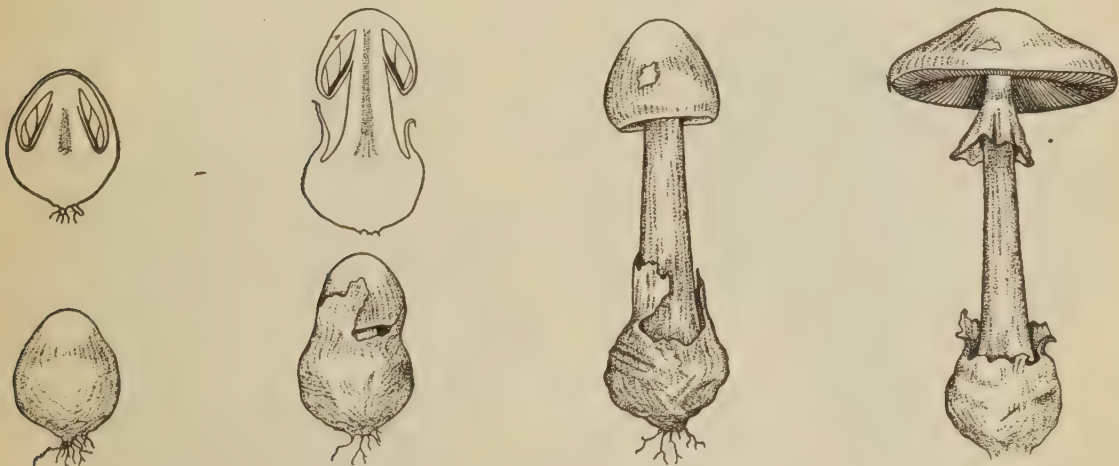


FIG. 381. Development of a gill fungus, the deadly amanita (*Amanita phalloides*)

Redrawn after Longyear

host or the æciospores may be found on one host and the urediniospores and teliospores on an entirely different host. One of the best-known and most destructive of the rusts is the wheat



FIG. 382. A pore fungus (*Fomes pachyphloeus*) on a tree trunk. ( $\times \frac{2}{15}$ )

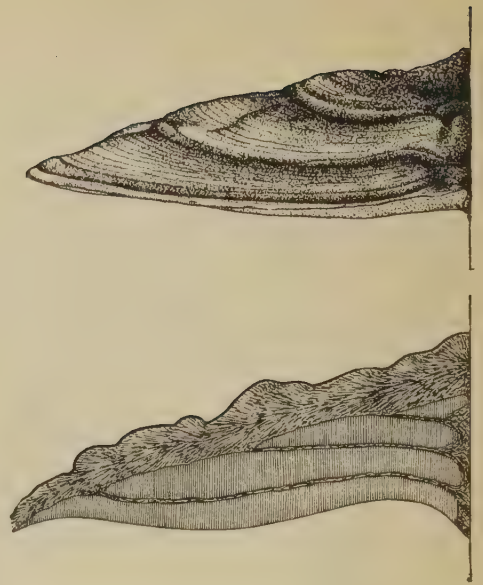


FIG. 383. Side view and section of a pore fungus (*Fomes pachyphloeus*)

The layers in the lower drawing show pores formed during successive seasons. ( $\times \frac{1}{3}$ )



FIG. 384. *Clavaria*

A basidiomycete in which the hymenium covers the coral-like branches. ( $\times \frac{2}{3}$ )

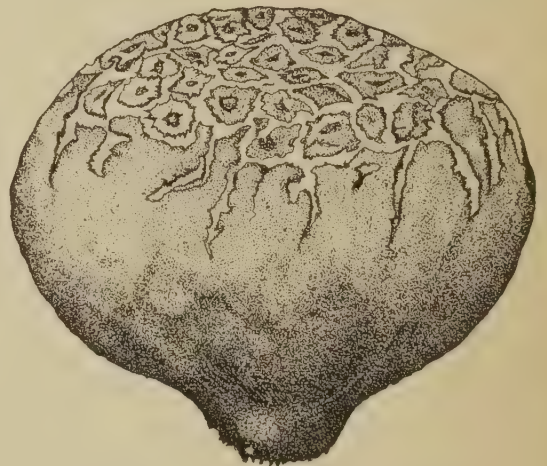


FIG. 385. Puffball (*Lycoperdon cyathiforme*)

Redrawn after Farlow. ( $\times \frac{1}{2}$ )





FIG. 386. *Geaster limbatus*

The sterile covering splits into two parts, one of which surrounds the spore mass while the other curves back, forming a star-shaped structure. ( $\times \frac{1}{2}$ )



FIG. 388. *Geaster hygrometricus*

Left, position when moist; right, position when dry. ( $\times \frac{1}{2}$ )



FIG. 390. *Dictyophallus*, a stinkhorn fungus

The ripe spores occur in a sticky mass on the cap which is above the veil. ( $\times \frac{1}{2}$ )



FIG. 387. Puffballs which have opened at the top. ( $\times 1\frac{1}{5}$ )



FIG. 389. *Cyathus striatus*, a bird's-nest fungus

The spore masses are inclosed in sterile ovoid coverings. ( $\times 1$ )



FIG. 391. *Ithyphallus*, a stinkhorn fungus. ( $\times \frac{1}{2}$ )

rust (*Puccinia graminis*). In this species the æciospores are found on barberry leaves (Fig. 374), and the urediniospores and

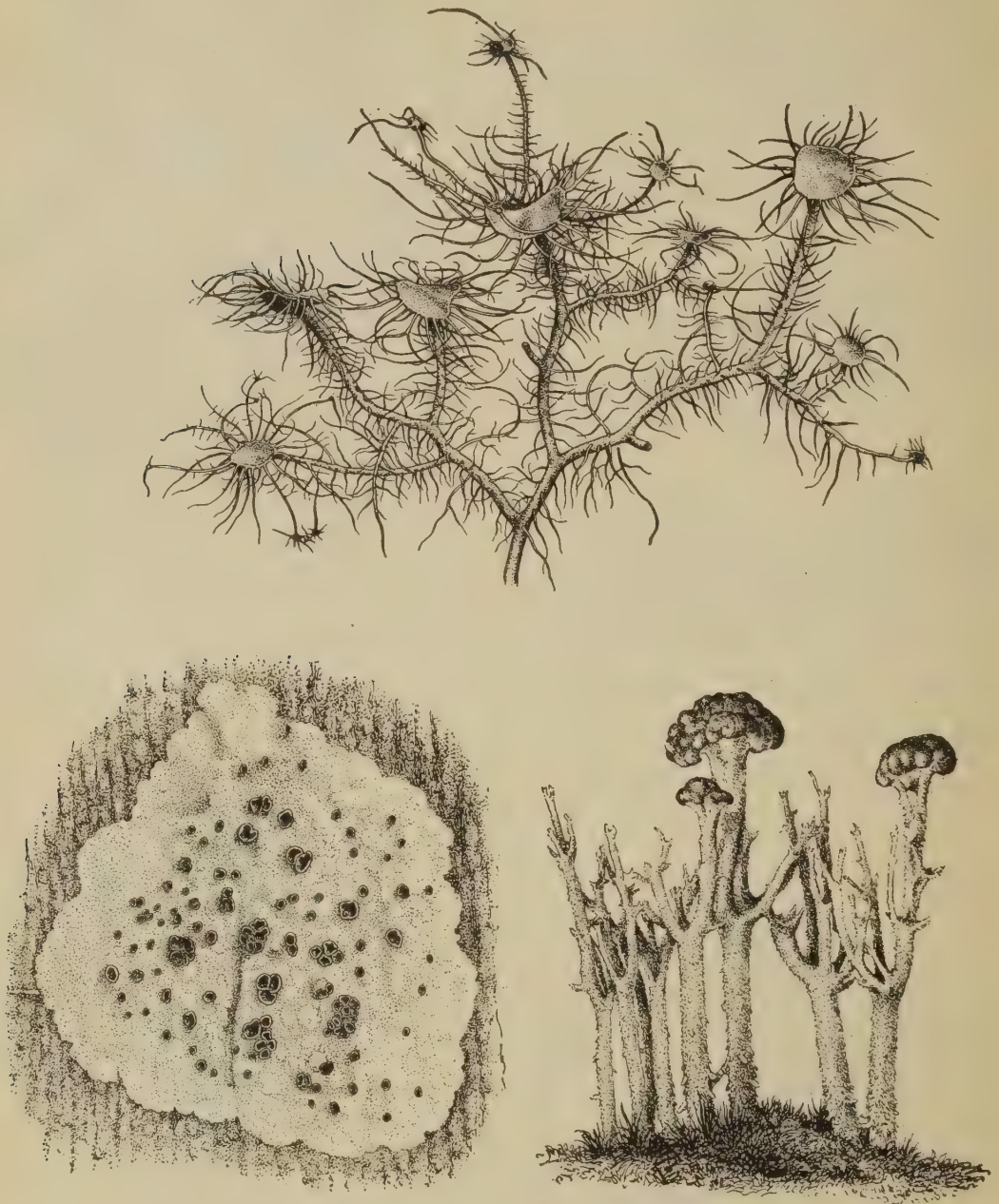


FIG. 392. Three forms of lichens

Above, *Usnea barbata*, a branched epiphytic form; lower left, *Haematomma puniceum*, a crustaceous form; lower right, *Cladonia furcata*, an erect terrestrial form. ( $\times 1$ )

the teliospores on wheat (Figs. 373, 377). As the basidiospores of *Puccinia graminis* do not infect wheat but only infect the barberry bush, this disease can be very largely controlled by



destroying barberry plants. Another very destructive rust is the coffee rust (Fig. 374), which has almost entirely destroyed the coffee industry in a number of countries in the eastern tropics.

**Eubasidii.** The *Eubasidii* contain the largest and most conspicuous of the fungi. The basidia are nonseptate, club-shaped structures which, typically, bear four spores (Fig. 370).

The *Eubasidii* contain two groups, the *Hymenomyces* and the *Gasteromyces*. In the *Hymenomyces* the basidia are borne in a layer, the hymenium, which is naked at maturity (Fig. 370). The most numerous of the *Hymenomyces* are the mushrooms (gill fungi) (Fig. 381) and the pore fungi (Figs. 382, 383). In the first case the hymenium covers the surface of gills, and in the second case lines numerous pores. In the *Gasteromyces* the spores are inclosed in a sterile covering. The group includes the puffballs (Figs. 385, 387), earthstars (Figs. 386, 388), bird's-nest fungi (Fig. 389), and stinkhorns (Figs. 390, 391). The last are evil-smelling fungi which are often strikingly colored and have fancy shapes (Figs. 390, 391). When mature the spores occur in a sticky mass on the cap of the fruiting body.



FIG. 393. *Lobaria pulmonaria*, a lichen with a thallus form and cup-shaped fruiting bodies. ( $\times 1$ )

**Economic importance of fungi.** Fungi are harmful in the following ways:

1. They cause great economic loss by producing plant diseases.
2. They cause diseases of animals, including man. Many skin diseases of man are due to fungi.

3. They destroy food, clothing, timber, and other useful materials.
4. Some fungi are poisonous and when eaten cause serious illness or even death.

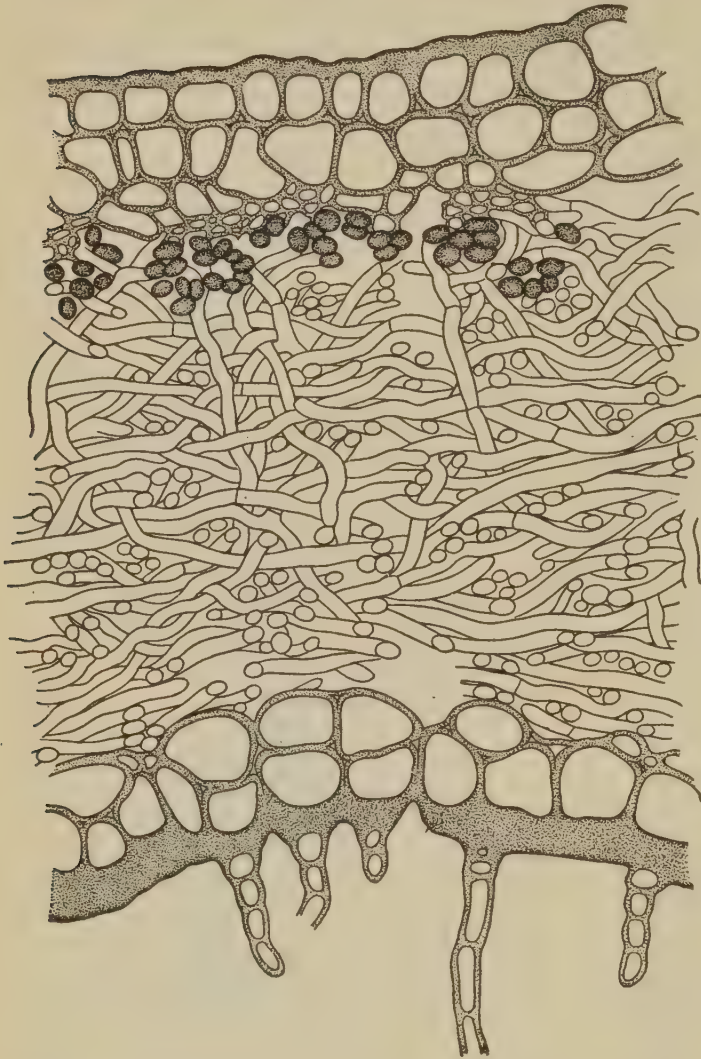


FIG. 394. Cross section of a lichen thallus

The dark oval bodies near the upper portion of the thallus are algal cells

Fungi are useful to man in the following ways:

1. Certain fungi, particularly mushrooms, are used for food. In some countries the raising of mushrooms is an industry of considerable importance. The flavors of many fine cheeses are due to the growth of fungi.

2. Some fungi are used as medicine, one, ergot (*Claviceps purpurea*) (Fig. 368), being official in all pharmacopœias.

3. All commercial alcohol is produced by the yeast fungi.

4. The raising of bread by yeast is due to the yeast fungus.

5. Certain fungi kill insects which are harmful to man. One fungus attacks the common house fly and is one of the few natural agents which reduce their number.

6. Fungi are useful by causing the decay of plant and animal remains. If it were not for the destruction of dead plants and animals by fungi and other organisms the remains of plants and animals would form a thick covering over the earth. By the decay of plants and animals the food material in them is rendered available to green plants.



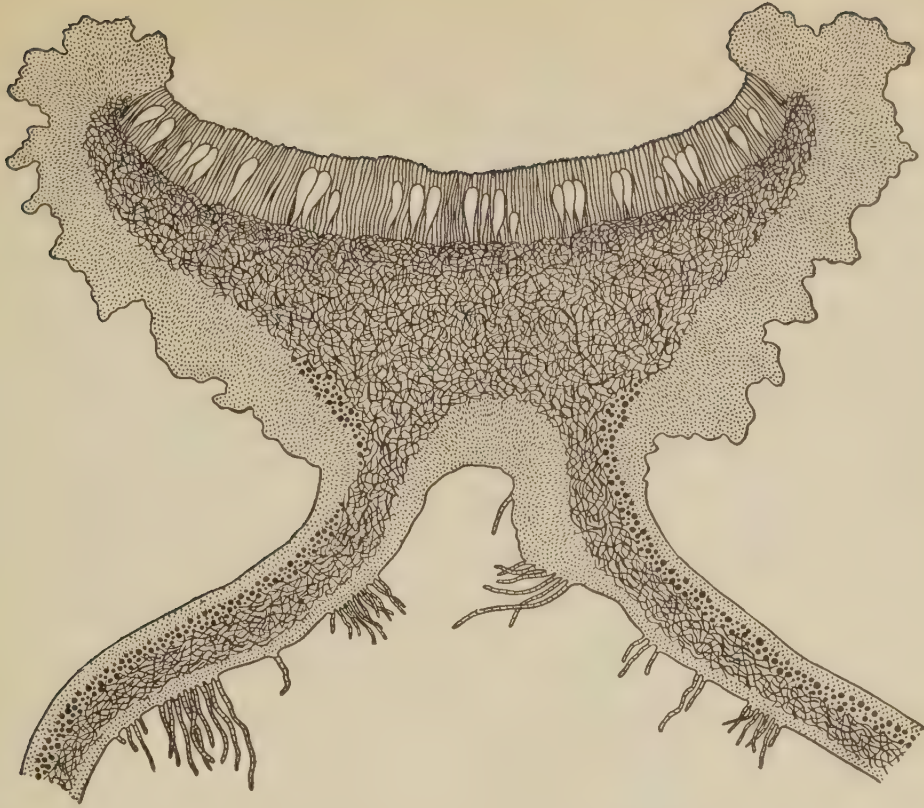


FIG. 395. Cross section through a whole lichen fruit body and portion of adjoining thallus

Note the algal cells showing as dark spots in the upper part of the thallus; note also the hymenium lining the cup. ( $\times 40$ )

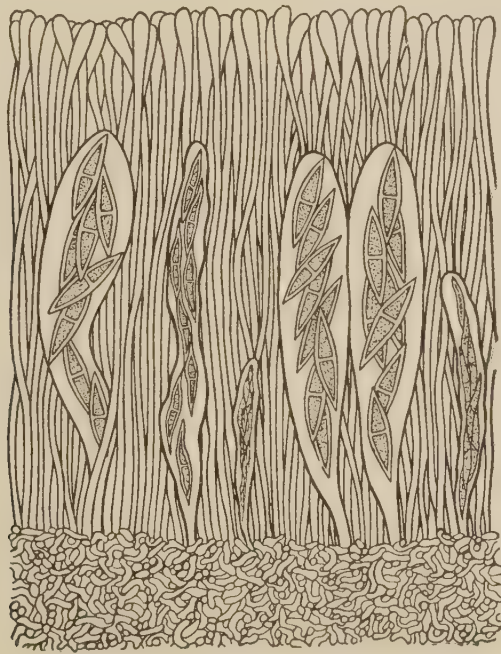


FIG. 396. Cross section of a portion of the hymenium of a lichen fruit body, showing asci and paraphyses. ( $\times 320$ )

## CLASS LICHENS

Lichens are thallus plants (Figs. 392, 393) the bodies of which are composed of interlacing fungus hyphæ, among which are found algal cells on which the fungus is parasitic (Fig. 394). Most lichens are greenish gray, the color being the result of a combination of the colors of the two components. In one genus of the lichens the fungus is a basidiomycete, while in the other genera the fungi are ascomycetes (Figs. 395, 396). The alga may be either *Chlorophyceae* or *Cyanophyceae*. The combination of fungus and alga is able to live in places, such as bare rocks, where neither of the constituents could survive alone. The habitat of lichens varies greatly. They may grow on rocks, or as epiphytes on branches or leaves, or on the ground. One of the lichens, the so-called reindeer moss, is abundant in northern latitudes and serves as food for reindeer and caribou.



## CHAPTER XI

### DIVISION *BRYOPHYTA*

The bryophytes are composed of two classes of plants, the *Hepaticae* (liverworts) and the *Musci* (true mosses). The bryophytes are small plants most of which grow in moist places, although some live in dry habitats and will revive after being dried. Bryophytes do not have roots but are anchored to the substratum by hair-like rhizoids. The mosses are differentiated into a central axis, or stem, and small, spirally arranged leaves (Fig. 418). Some of the liverworts are thallus plants (Fig. 397), while others have stems and delicate leaves (Fig. 413). In those with stems and leaves there are two dorsal rows of leaves arranged along the sides of the stem, and usually a third small row on the ventral surface. The leaves of most mosses have

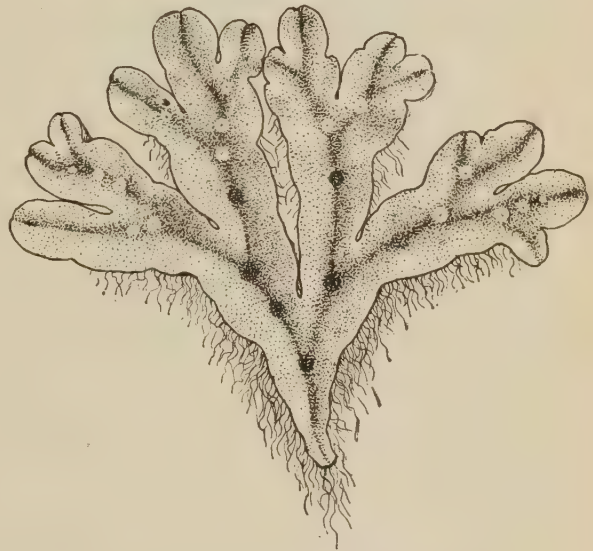


FIG. 397. Thallus of *Riccia*

The dark rounded bodies are mature sporophytes which are embedded in the thallus, while the lighter bodies are immature sporophytes. ( $\times 2$ )

a midrib, while such a structure is not found in any of the liverworts. The female reproductive organ of the bryophytes is an *archegonium* (Fig. 399). This is a flask-shaped structure which, when mature, contains a single egg. Spermatozoids are borne in large numbers in *antheridia* (Fig. 400). The development of the fertilized egg results in the production of a *sporophyte*, which, in most cases, consists of a sporangium, or capsule, a stalk,

and an absorbing organ, or foot, which absorbs material from the parent plant (Fig. 410). In a few species of simple liverworts the sporophyte is a sporangium without stalk or foot (Figs. 401, 402).

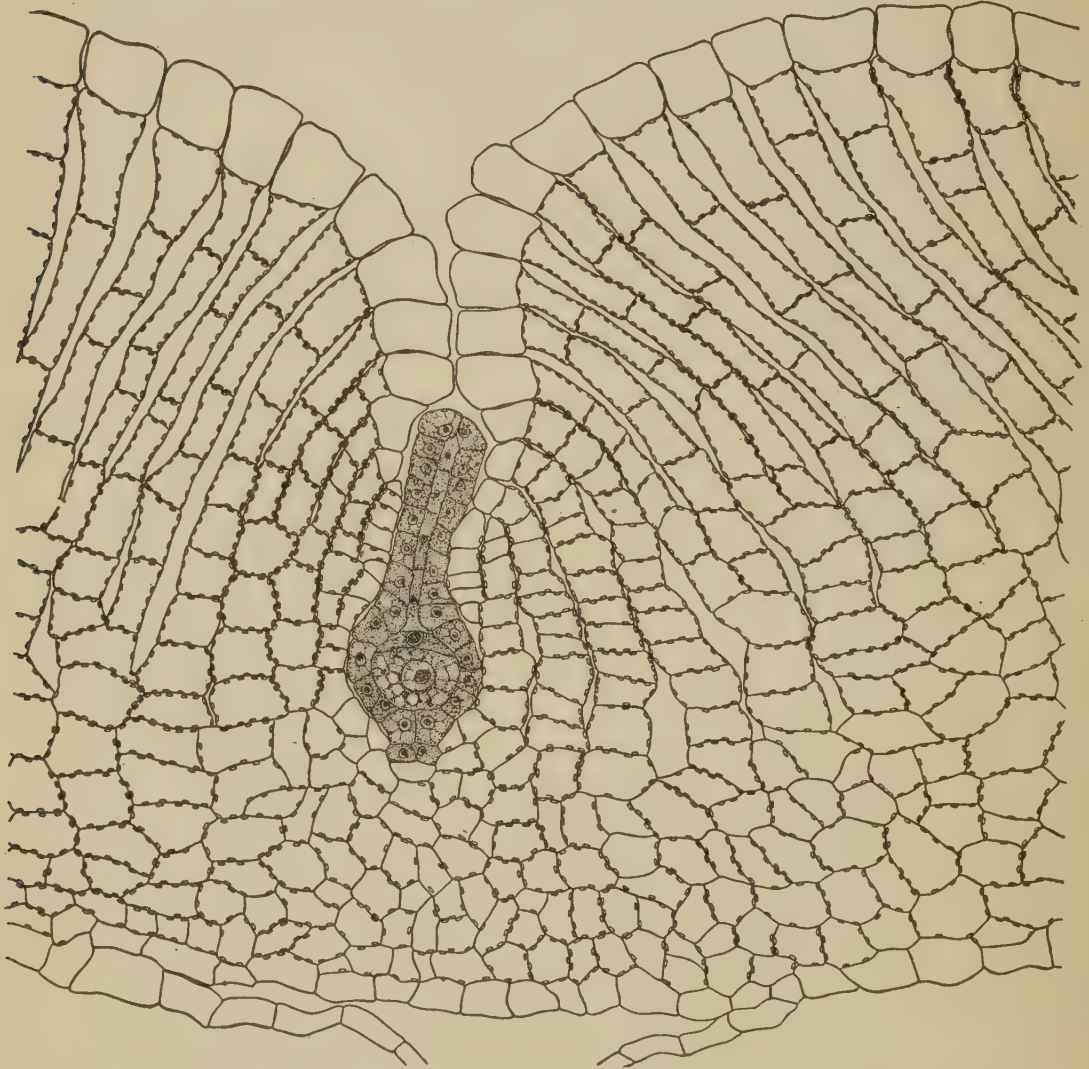


FIG. 398. Section of a portion of the thallus of *Riccia*

In the center is an immature archegonium ; the enlarged venter contains a large egg and above this a ventral-canal cell ; in the neck there are four neck-canal cells. ( $\times 190$ )

#### CLASS HEPATICAE

**Gametophyte.** Most of the *Hepaticae* live on the land in moist places, while a few grow in water. Some of them are found on the ground and others on the trunks or leaves of other plants.



The conspicuous stage in the life history is known as the *gametophyte* (Fig. 397), because it produces gametes. These are of two kinds, eggs and spermatozoids. The eggs are borne in flask-shaped oögonia, called archegonia (Fig. 398). An archegonium of a liverwort is a flask-shaped structure, the wall of

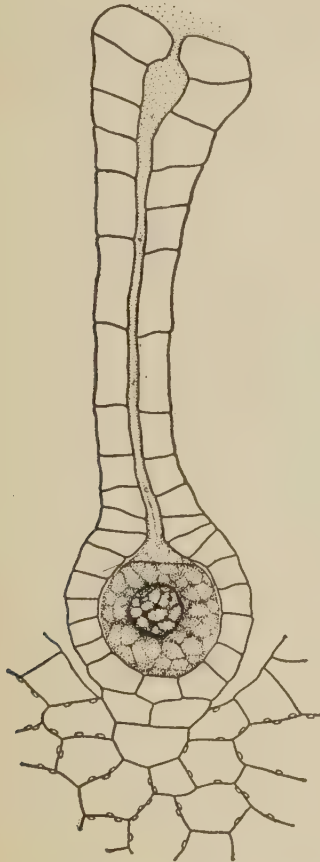


FIG. 399. Mature archegonium of *Riccia*

The neck-canal cells and ventral-canal cell have become disorganized. ( $\times 240$ )

is a large *egg*, while the upper is smaller and is known as the *ventral-canal cell* (Fig. 398). The upper portion of the archegonium is elongated into a narrow structure called the *neck*. Within the neck is a row of *neck-canal cells* (Fig. 398). When the archegonium matures, the ventral-canal cell and neck-canal cells become disorganized and the top of the neck opens to discharge the remains of the canal cells (Fig. 399), after which the sperm can swim through the neck to the egg cell. The anther-

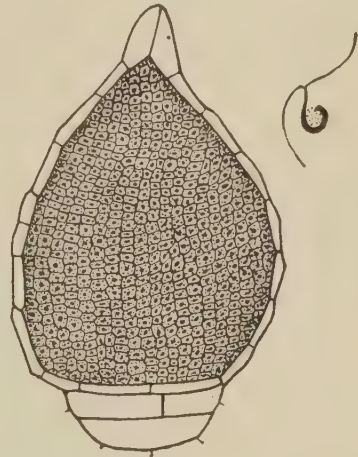


FIG. 400. Antheridium ( $\times 160$ ) and a single spermatozoid of *Riccia*

The antheridium consists of a stalk, a covering of sterile cells, and many sperm cells

which is composed of a single layer of cells. The lower part of the archegonium is enlarged and contains a single large cell which, shortly before the archegonium matures, divides into two cells, the lower of which

idium of a liverwort is usually somewhat oval and consists of an inner portion, composed of numerous sperm cells, surrounded by a single layer of sterile cells (Fig. 400). Each of the sperm cells

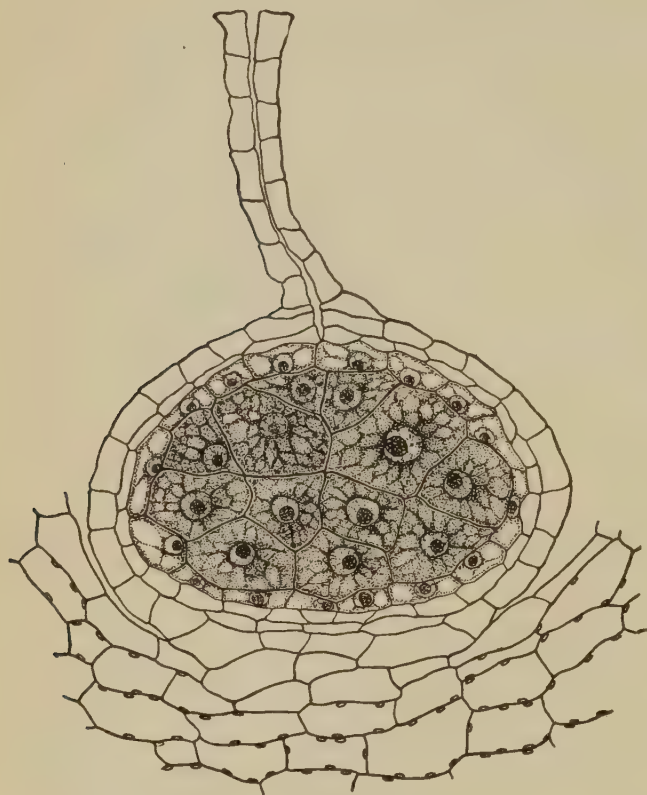


FIG. 401. Immature sporophyte of *Riccia* within the archegonium

The cells of the basal portion, or venter, of the archegonium have divided, so that this part of the archegonium consists of two layers of cells. At this stage the sporophyte consists of a considerable number of megaspore mother cells surrounded by a single layer of sterile cells. The nuclei and protoplasm are shown in the sporophyte and not in the tissue of the gametophyte. ( $\times 140$ )

but, instead of giving rise to a thallus, produces a structure in which spores are formed (Fig. 401). This spore-bearing structure is known as a sporophyte. The spores, on germination, produce a gametophyte. The sporophyte, in its simplest form, consists of a single sporangium (Figs. 401, 402), while in most of the *Hepaticae* it is a sporangium with a stalk and

produces a single ciliated spermatozoid (Fig. 400).

Fertilization takes place by the swimming of a spermatozoid to the egg in the archegonium and the fusion of the spermatozoid with the egg. Owing to the fact that the spermatozoids have no other means of reaching the archegonia than by swimming through water, it is evident that water is necessary for the accomplishment of fertilization. This indicates that the *Hepaticae* are descended from an algal ancestor, which lived in water and in which fertilization was also accomplished by means of motile spermatozoids.

**Sporophyte.** The fertilized egg of the *Hepaticae* germinates immediately within the archegonium,



an absorbing organ, the foot, which attaches the sporophyte to the gametophyte (Fig. 410).

**Alternation of generations.** The gametophyte that bears eggs and sperms is followed by a sporophyte that produces spores, and this in turn by a gametophyte. There is, therefore, an alternation between a gametophyte, that bears eggs and sperms, and a sporophyte, that produces spores. This alternation of

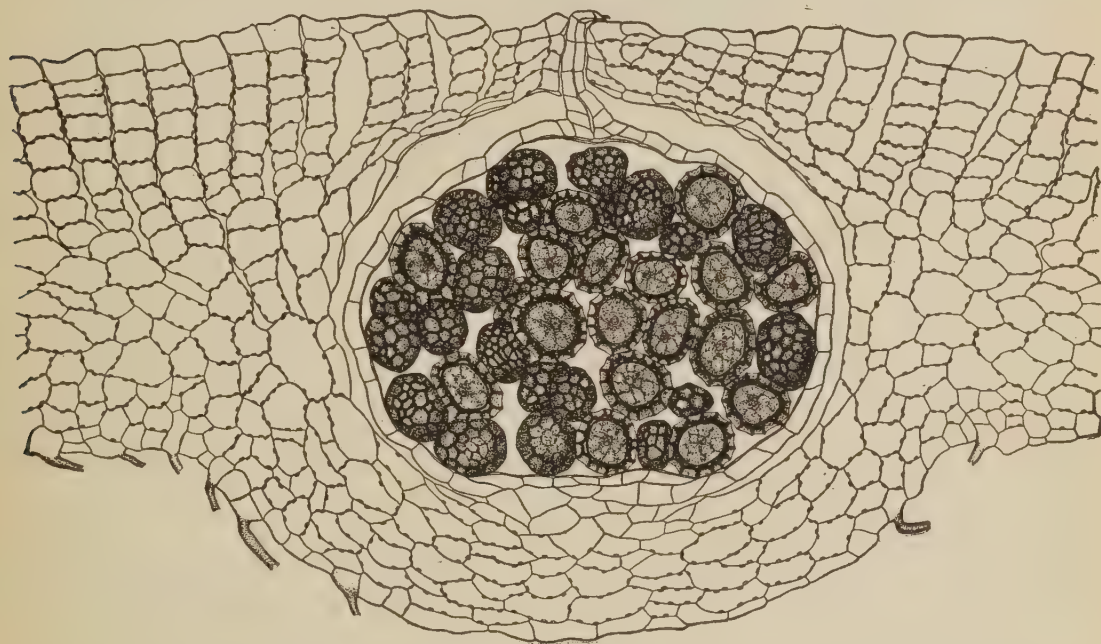


FIG. 402. Section of thallus of *Riccia*, showing mature sporophyte

The sporophyte, or sporangium, at this stage consists of a mass of spores, the sterile covering having disappeared. The spores lie free in the venter of the archegonium, the inner layer of cells of which has practically disappeared. ( $\times 80$ )

gametophytes and sporophytes is known as the alternation of generations or the alternation of gametophytic and sporophytic generations (Fig. 438).

As a result of the fusion of the nuclei of the egg and spermatozoid the fertilized egg has twice as many chromosomes as either the egg or the spermatozoid. In other words, the egg or the spermatozoid has an  $x$  number of chromosomes, while the fertilized egg has a  $2x$  number. The  $2x$ , or double, number persists in the sporophyte until spore mother cells are formed. Each spore mother cell, by two successive divisions, gives rise

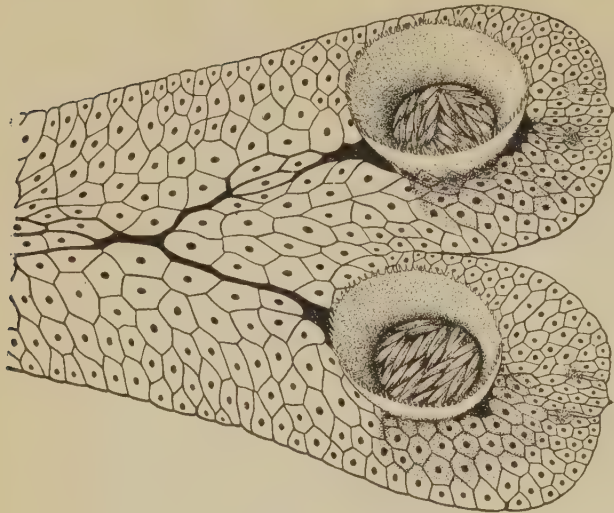


FIG. 403. Portion of a thallus of *Marchantia* bearing two gemma cups within which are many gemmæ

*Marchantia* reproduces asexually by the formation of lenticular gemmæ in gemma cups. These gemmæ produce new plants (Fig. 404). The lines dividing the thallus into polygonal areas mark the boundaries of air chambers, while the black dots represent the stomata-like openings into the chambers. ( $\times 6$ )

phytic and a sporophytic generation but also an alternation of a generation with a single and a generation with a double number of chromosomes.

**Orders of the *Hepaticeae*.** The *Hepaticeae*, or liverworts, contain four orders: the *Ricciales*, the *Marchantiales*, the *Jungermanniales*, and the *Anthocerotales*.

#### ORDER *RICCIALES*

The genus *Riccia* may be taken as an example of this order. The gametophyte is a dichotomously branching thallus (Fig. 397). Dichotomous branching is a system of branching in which the main axis forks repeatedly into

to four spores, and in the first of these two divisions the number of chromosomes is reduced. Thus each spore has a single number of chromosomes. These give rise to gametophytes with a single number of chromosomes, and the double number is again restored when the egg is fertilized by a spermatozoid. The gametophyte is thus characterized by a single number of chromosomes and the sporophyte by a double number. The alternation of generations is therefore not only an alternation of a gameto-

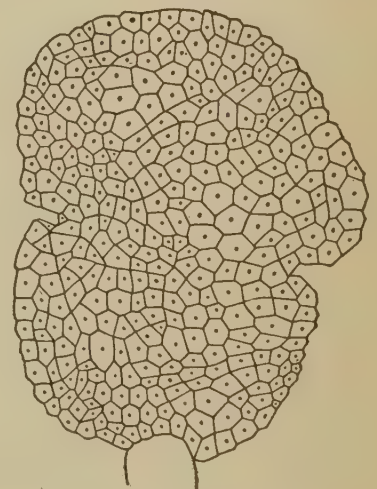


FIG. 404. Gemma of *Marchantia* after the rupture of stalk cell. ( $\times 150$ )



two equally developed parts. The archegonia (Fig. 399) and the antheridia (Fig. 400) are borne in a groove which extends longitudinally through the center of the upper part of the thallus (Figs. 397, 398). The fertilized egg develops inside of the archegonium. It gives rise to a single rounded sporangium without a stalk (Fig. 401). This sporangium consists of an outer layer of sterile cells and numerous spores. The sporangium wall is an evanescent structure which almost entirely disappears before the spores are mature,

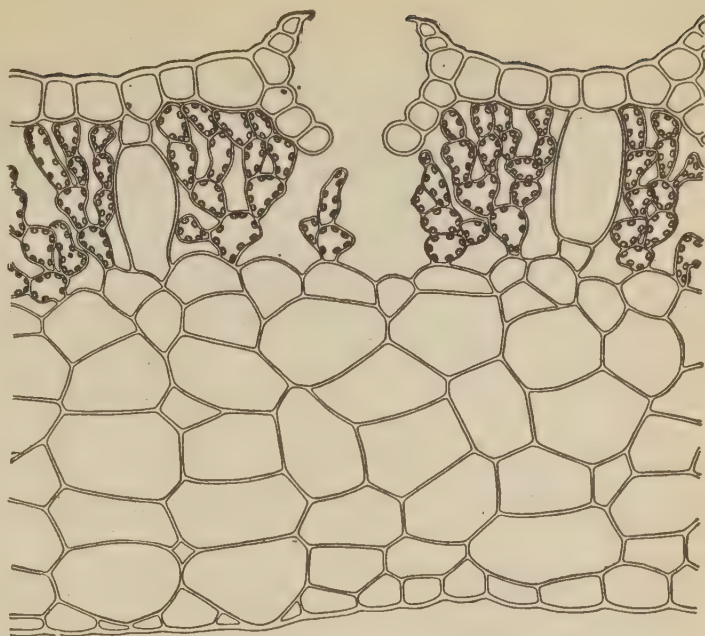


FIG. 405. Section of a portion of a thallus of *Marchantia*

Below, colorless tissue; above, air chambers with photosynthetic cells. Note the stomalike opening into the central chamber and the large cells which form the side walls of the chambers. ( $\times 200$ )

The sporangium wall is an evanescent structure which almost entirely disappears before the spores are mature,

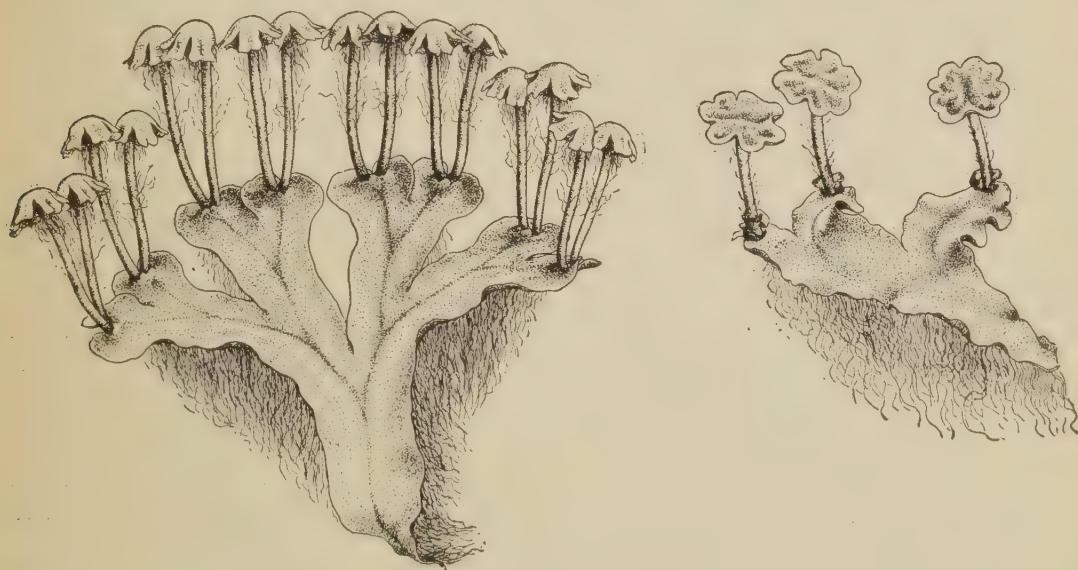


FIG. 406. *Marchantia*

Left, female plant with specialized branches which bear archegonia on their under surfaces; right, male plant with specialized branches which bear antheridia sunken in the upper surface. ( $\times 1\frac{1}{2}$ )

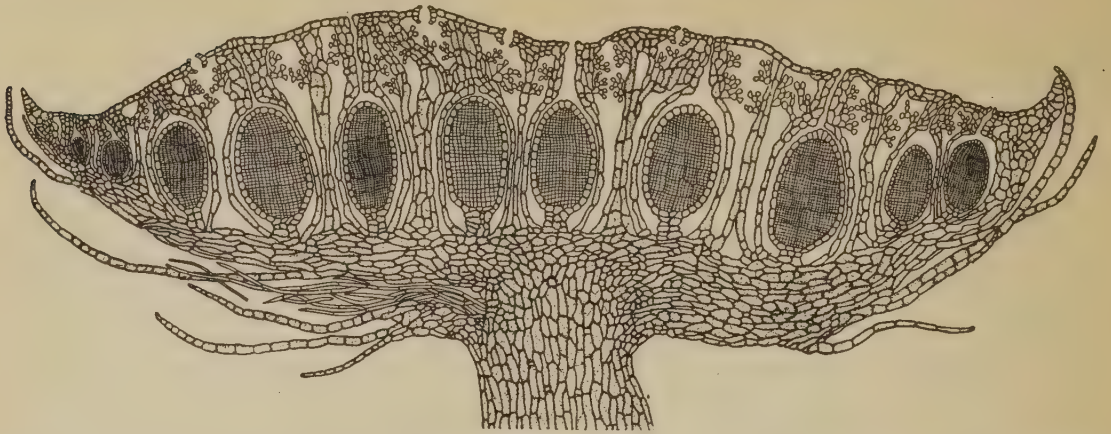


FIG. 407. Section through an antheridial branch of *Marchantia*, showing air chambers, and also ovoid antheridia containing many sperm cells. ( $\times 30$ )

so that the mature spores lie free in the cavity of the enlarged archegonium (Fig. 402). The mature sporangium is therefore

nothing more than a mass of spores (Fig. 402). The sporophyte of the *Ricciales* is the simplest one found in the bryophytes. When a spore germinates, it produces a thallus bearing archegonia and antheridia.

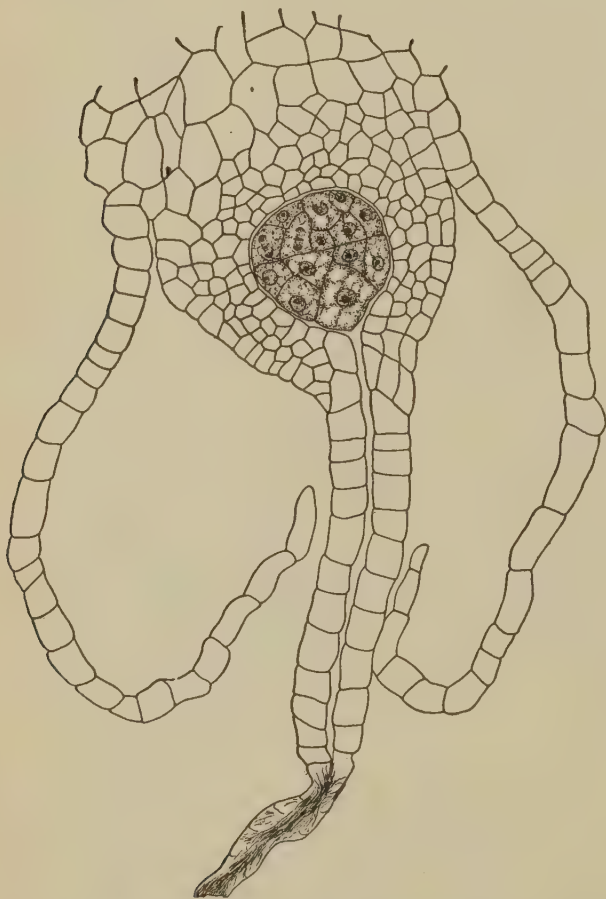


FIG. 408. Young sporophyte of *Marchantia* inclosed within an archegonium

The tip of the archegonium is disorganizing.  
( $\times 135$ )

#### ORDER *MARCHANTIALES*

The thallus of this order is much more complicated (Figs. 403-405) than that of the *Ricciales*. In the genus *Marchantia*, which may be taken as an example, the antheridia and the archegonia are borne on separate plants on special, upright, umbrella-like branches. The archegonia (Fig. 409) are found on



the lower surfaces of special branches which grow on female plants (Fig. 406), while the antheridia (Fig. 407) are sunk in the upper part of somewhat similar branches on male plants

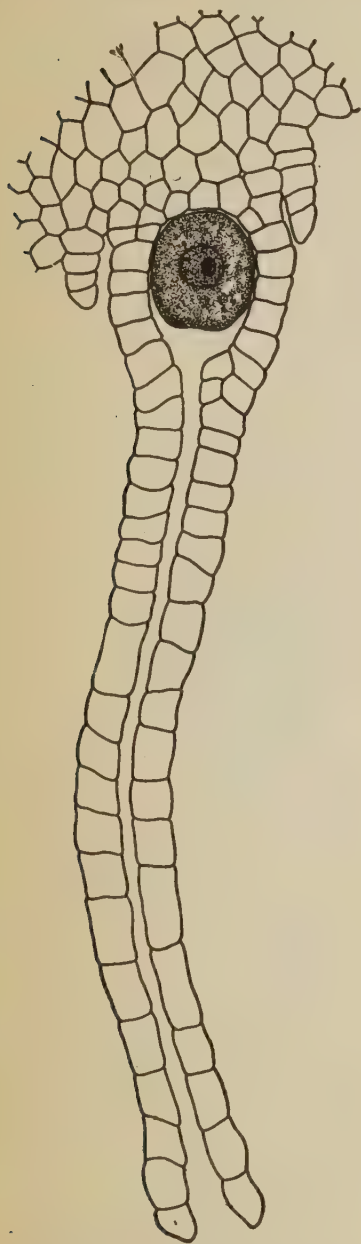


FIG. 409. Archegonium of *Marchantia*. ( $\times 175$ )

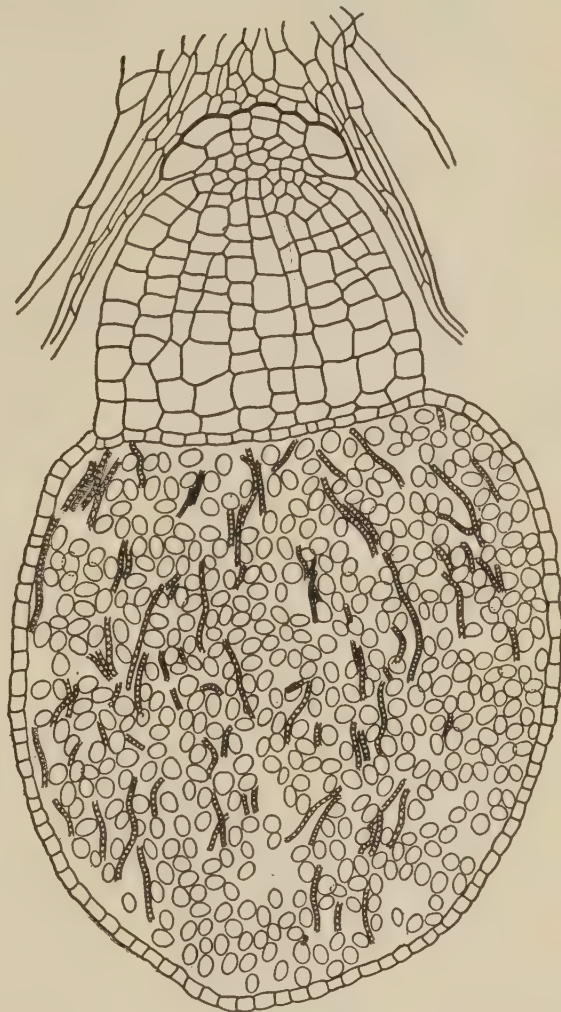


FIG. 410. Sporophyte of *Marchantia* before elongation of the stalk

Below is the large sporangium ; above this is the stalk, and above the stalk, the foot embedded in the archegonium. The upper limit of the foot is shown as a dark line. ( $\times 85$ )

(Fig. 406). The antheridia and archegonia (Fig. 409) are very similar to those of the *Ricciales*. The fertilized egg germinates within the archegonium (Fig. 408) and develops into a *sporophyte* (Figs. 410, 411). This consists of a rounded *sporangium*, an elongated *stalk*, and an absorbing structure, the *foot*, which

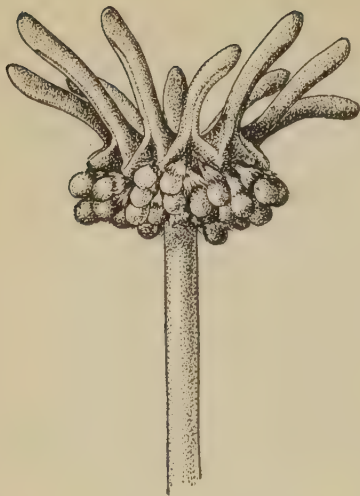


FIG. 411. Vertical branch of female thallus of *Marchantia* with many sporophytes. ( $\times 2\frac{1}{2}$ )

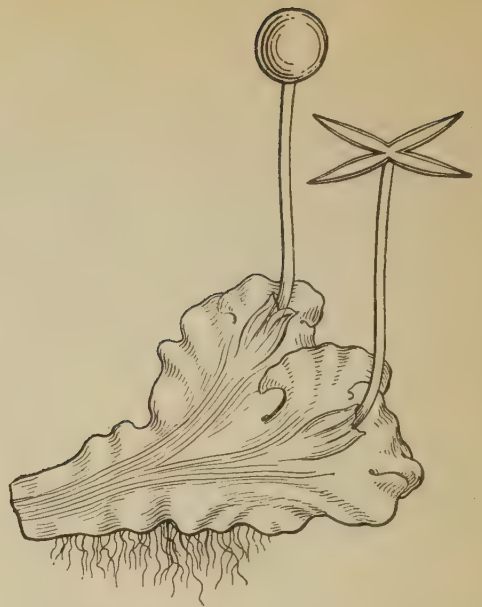


FIG. 412. Thallus of *Pellia* (one of the *Jungermanniales*) with unopened and opened sporophyte. ( $\times 2$ )



FIG. 413. Leafy liverworts

In the drawing at the left each leaf consists of a large and a small lobe; on the left side there is a sporophyte which has elongated out of the perianth and has opened; above this sporophyte is another which is still inclosed within the perianth ( $\times 4$ ). In the drawing at the right, each leaf consists of a large and a small lobe ( $\times 1$ )

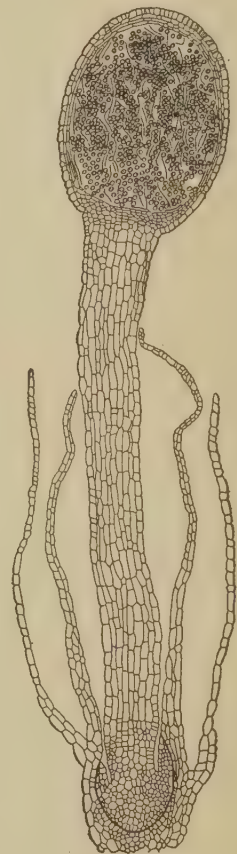


FIG. 414. Longitudinal section through sporophyte of *Ptilidium*, one of the *Jungermanniales*

The sporophyte consists of a sporangium, stalk, and foot, ( $\times 20$ )



is embedded in the tissue of the special upright branch of the thallus. When a spore germinates, it gives rise to a thallus producing archegonia and antheridia.

The *Marchantiales* are generally considered to be closely related to the *Ricciales*. The gametophytes of this order are the most

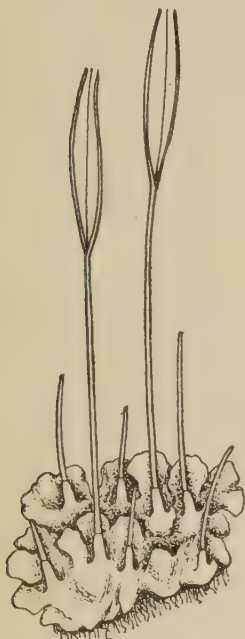


FIG. 415. Thallus of *Anthoceros* with six young unopened sporophytes and two long sporophytes which have split and show the columellae in the center. ( $\times 1\frac{1}{3}$ )

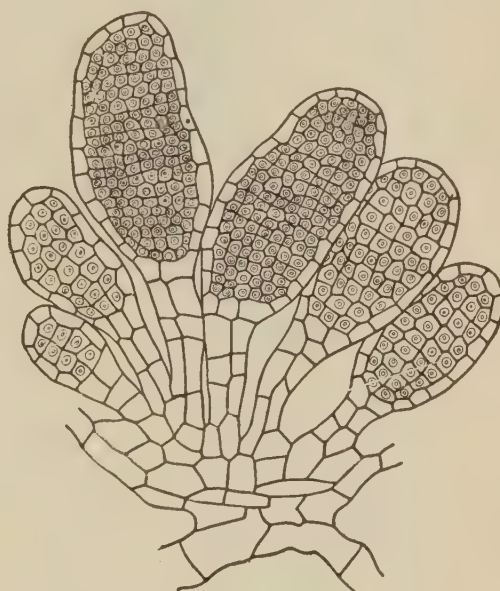


FIG. 416. A group of antheridia of *Anthoceros*

Each antheridium consists of a stalk, a covering of sterile cells, and many sperm cells. ( $\times 215$ )

highly specialized among the *Hepaticae* and are very different from those found in any other group of plants. From this it would appear that the *Marchantiales* represent a special line of evolution in which there has been a considerable development of the gametophyte.

#### ORDER *JUNGERMANNIALES*

Some of the members of this order have a simple thallus (Fig. 412), but in most cases the thallus is differentiated into stems and leaves (Fig. 413). The stems do not show a differentiation of tissues and have no specialized conducting cells. A leaf consists of a single layer of cells without a midrib. The

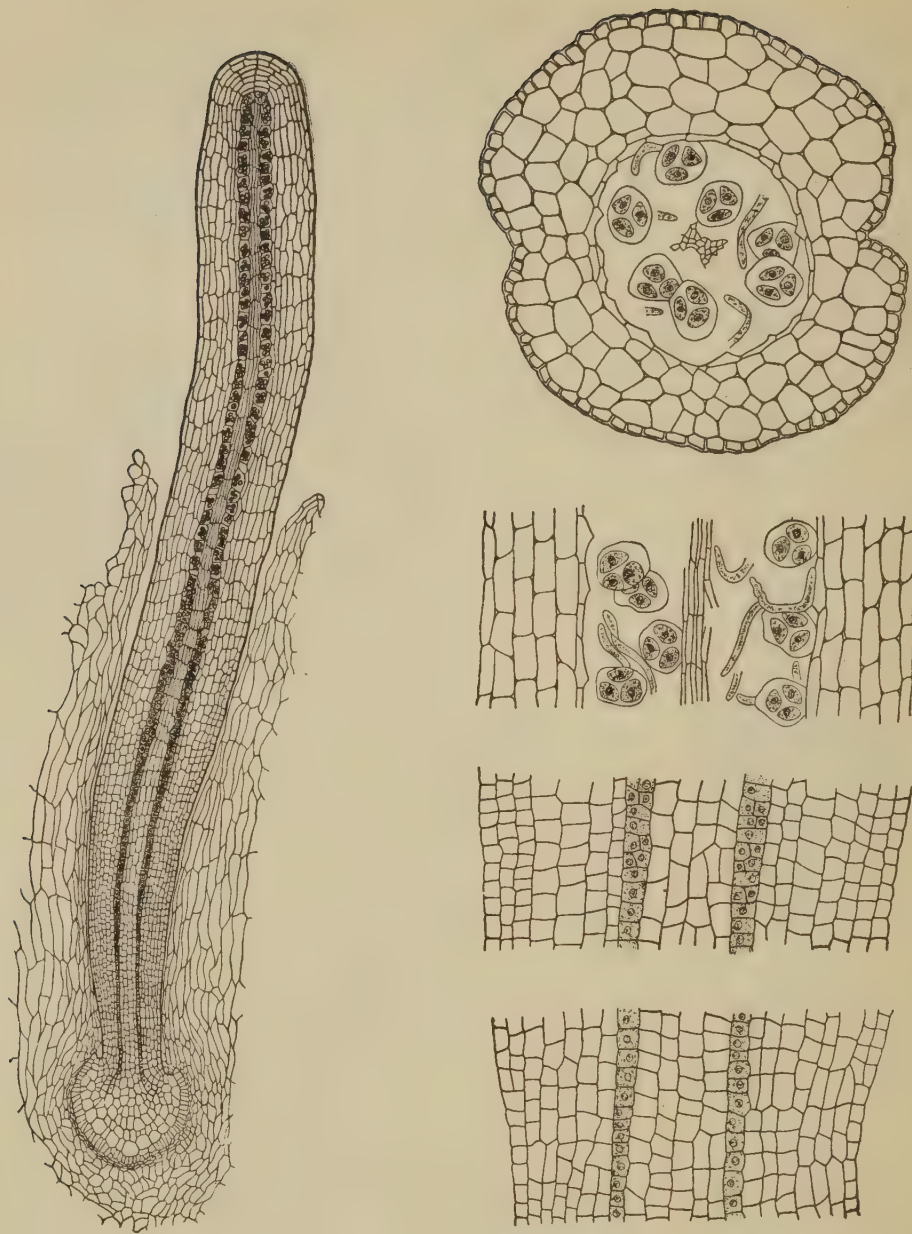


FIG. 417. *Anthoceros*

Left, section through sporangium and surrounding portion of thallus ( $\times 31$ ). The lower part of the sporophyte is a foot, above this is a meristematic region, and still higher up are progressively older stages in the formation of spores. Note the sterile columella in the center and the sterile tissue surrounding the spore-bearing portion. In the drawing the sporogenous tissue is darker than the sterile tissue. Right: upper drawing, cross section of sporangium showing columella in the center surrounded by sporogenous region; the lower drawings show successive stages in spore formation as seen in longitudinal section ( $\times 105$ )



archegonia and the antheridia are similiar to those of the two previous orders. The fertilized eggs develop into a sporophyte (Fig. 414) similar to that of the *Marchantiales* in that it consists of a sporangium, a foot, and a stalk.

The sporophyte of the *Jungermanniales* is more complex than that of the *Ricciales*, but the simplest thalli found among the *Hepaticae* occur in some of the thallus members of this order.

#### ORDER ANTHOCEROTALES

The thallus of the *Anthocerotales* is simple, but the sporophyte is more complicated than that of any other order. *Anthoceros* (Fig. 415) may be taken as an example. In this genus the sporophyte (Fig. 417) consists of a basal absorbing organ, the foot, and a terminal club-shaped sporangium. Near the base there is a meristematic region, the activity of which causes the sporangium to increase in length. The outer part of the sporangium consists of sterile cells, and in the center there is a column of sterile cells, the columella. The spores are formed between these two sterile regions. As the spores in the tip of the sporangium reach maturity the upper part of the sporangium splits and the spores are liberated (Fig. 415). As more spores mature the sporangium continues to split. In this way the sporangium is continually liberating spores, while new spores are being produced as the result of the activity of the basal meristem.



FIG. 418. Gametophyte of a moss, showing a group of antheridia and archegonia at the tip. ( $\times 7$ )

While the thalli of the *Anthocerotales* are simple, the sporophytes are the most complex found in the *Hepaticae*. They resemble the sporophytes of the *Musci*, and also those of the *Pteridophyta* and *Spermatophyta*, in having stomata and assimilating tissue with chlorophyll. Owing to the presence of chlorophyll the sporophyte is only partially dependent on the gametophyte. If the foot of the sporophyte of *Anthoceros* were developed into a root, the sporophyte would be an independent plant.



FIG. 419. A single archegonium of a moss. ( $\times 150$ )

The gametophytes bear archegonia (Fig. 419) and antheridia (Fig. 420), which may be on the same or on different plants. They occur in groups at the tips of the stems (Figs. 418, 421).

The fertilized egg develops and produces a *sporophyte* (Fig. 422), which usually, like those of most liverworts, consists

#### CLASS MUSCI

**Life history.** The mosses are a large group of small plants which, like the liverworts, are characterized by an alternation of a gametophyte and a sporophyte.

The gametophyte is a leafy plant (Fig. 418). In most cases the stem contains conducting tissue and the leaf a midrib. The gametophytes bear

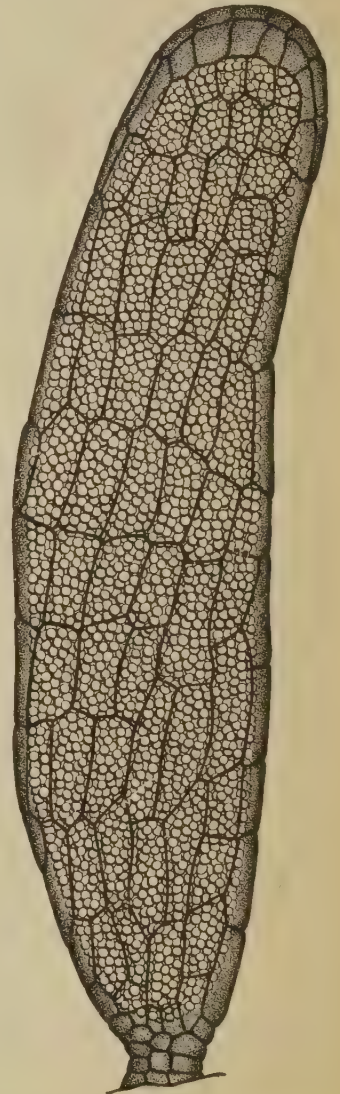


FIG. 420. A single antheridium of a moss. ( $\times 155$ )



of a *foot*, a *stalk*, and a *sporangium*. The last is a complicated structure, frequently spoken of as the moss capsule. It resembles the sporophyte of the *Anthocerotales* in having assimilating

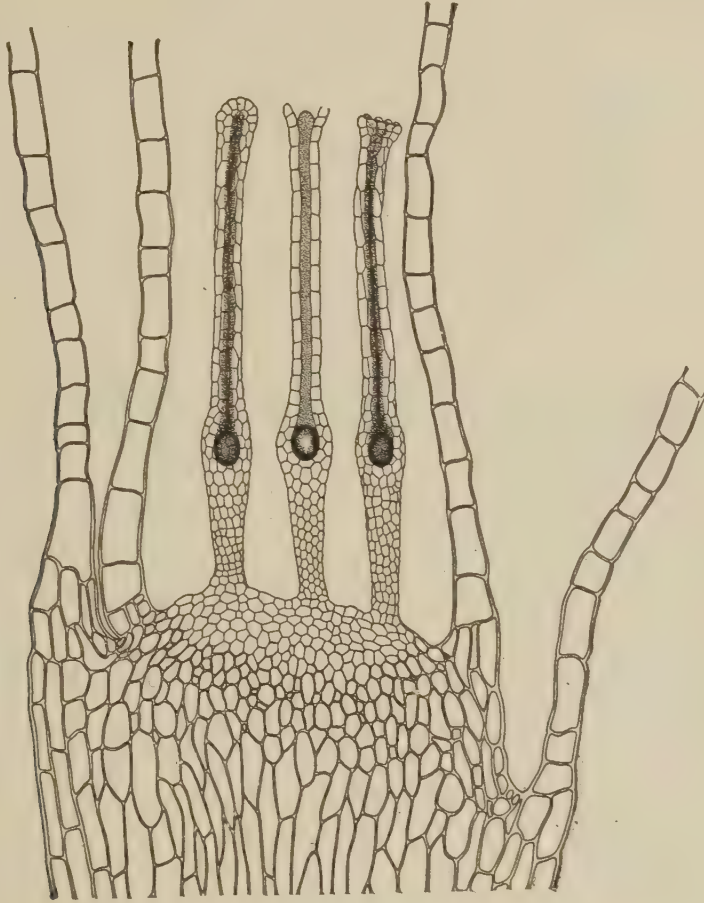


FIG. 421. Section through a tip of a moss plant, showing location of archegonia

The archegonium on the left has not yet opened ; the one in the center is shown in section. ( $\times 80$ )

tissue containing chlorophyll and in possessing stomata of the type which is found in the *Pteridophyta* and *Spermatophyta*.

**Relationship.** The mosses are closely related to the liverworts and appear to have been derived from them. While the sporophytes of the mosses and the *Anthocerotales* are very different in structure, there are similarities which indicate that mosses are more closely related to the *Anthocerotales* than to any of the other liverworts.



FIG. 422. Gametophyte of a moss

Left, a moss gametophyte bearing a sporophyte; note that the sporangium, or capsule, is covered by a hood, or calyptra, which was originally a part of the archegonium wall ( $\times 1\frac{2}{3}$ ). Upper right, a capsule with calyptra removed; the upper portion is differentiated into a lid, or operculum. Below this figure is shown a capsule with the operculum removed; note the fringe of toothlike appendages known as the peristome ( $\times 3$ )

Mosses are much more numerous than liverworts, both in species and in individuals, but they are much more uniform in structure.

**Peat mosses.** Mosses are a prominent constituent of peat bogs. These occur in depressions containing fairly still water. The mosses grow in from the sides and form a floating mass. As the mosses and other plants associated with them continue to grow upward the lower layers are forced downward, and dead plant remains, known as *peat*, accumulate under the living cover. In the course of time the depression is filled, but the mosses, owing to their ability to absorb and hold large quantities of water, may continue to grow until the bog is raised considerably above its original level and even above the level of the surrounding area. The lower layers of plant remains become compressed and partially carbonized, forming peat. The layers of peat are cut into blocks and used as fuel. The peat is sometimes treated so as to improve its value as a fuel.

Coal was formed by a process somewhat similar to that which gives rise to peat. The plants were different and their remains accumulated not in bogs but as muck in the swamps or open waters of past ages.

*Sphagnum*, the chief peat moss, is used extensively for packing plants and in surgical dressings.



## CHAPTER XII

### DIVISION *PTERIDOPHYTA* (FERNS AND FERN ALLIES)

The pteridophytes are characterized by the alternation of two distinct kinds of plants: a *gametophyte*, or *prothallus*, which is a small thallus bearing archegonia or antheridia, or both (Fig. 432);



FIG. 423. A group of large tree ferns (*Cyathea*) in a mountain forest in the Philippines

and a *sporophyte*, which develops from the fertilized egg of a gametophyte and is differentiated into stems, roots, and leaves, and bears sporangia containing spores (Figs. 423, 424). On germination these spores give rise to the thallus gametophyte, or prothallus.



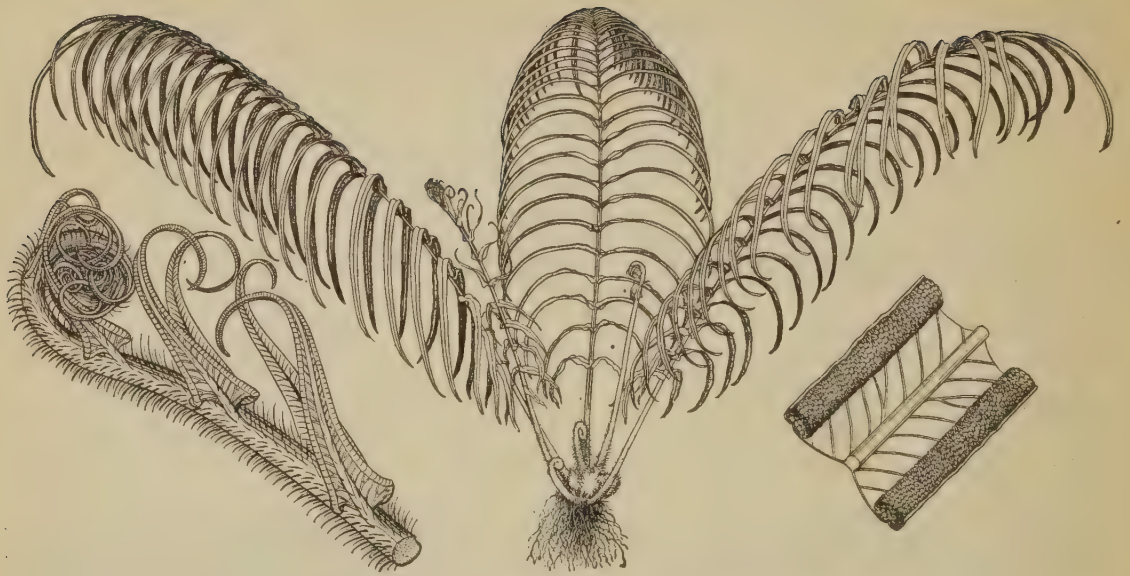


FIG. 424. Sporophyte of *Pteris longifolia* ( $\times \frac{1}{10}$ )

On the left is the tip of a young leaf which is unrolling ( $\times 1$ ); on the right, the under surface of a fertile pinna, showing sporangia aggregated near the sides ( $\times 2$ )

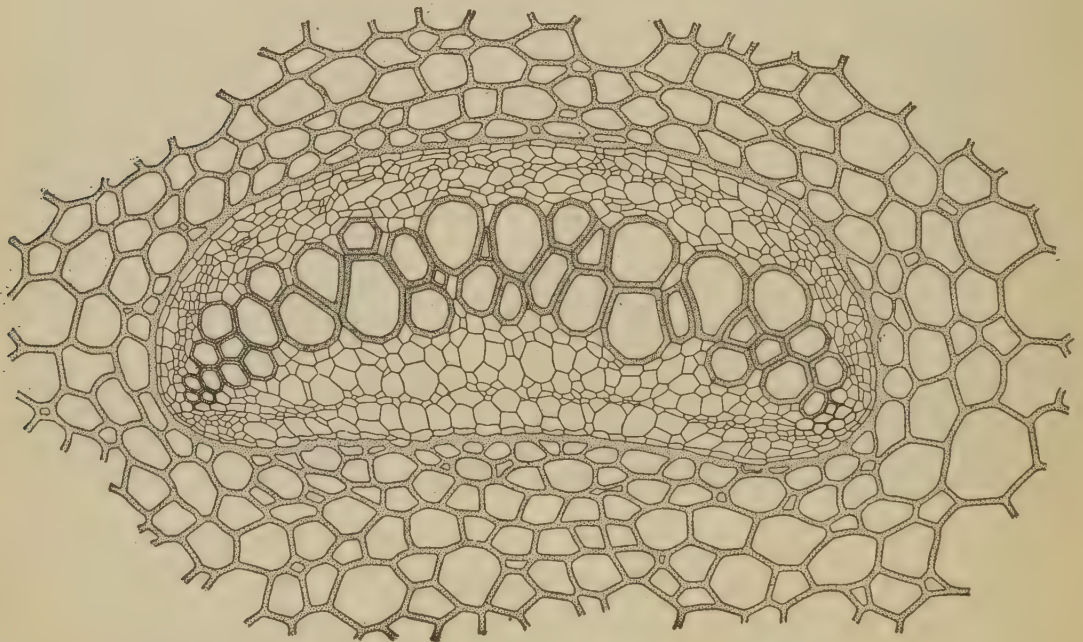


FIG. 425. Section of a concentric vascular bundle of a fern (*Davallia solida*)  
Note that the xylem is surrounded by the phloëm. ( $\times 110$ )



The *Pteridophyta* are divided into three classes: *Filicineae* (ferns), *Equisetineae* (horsetails), and *Lycopodineae* (club mosses).

CLASS *FILICINEAE* (FERNS)

**Sporophyte.** The sporophyte of ferns (Fig. 423) varies greatly in size, ranging from small mosslike species to the tall tree ferns.

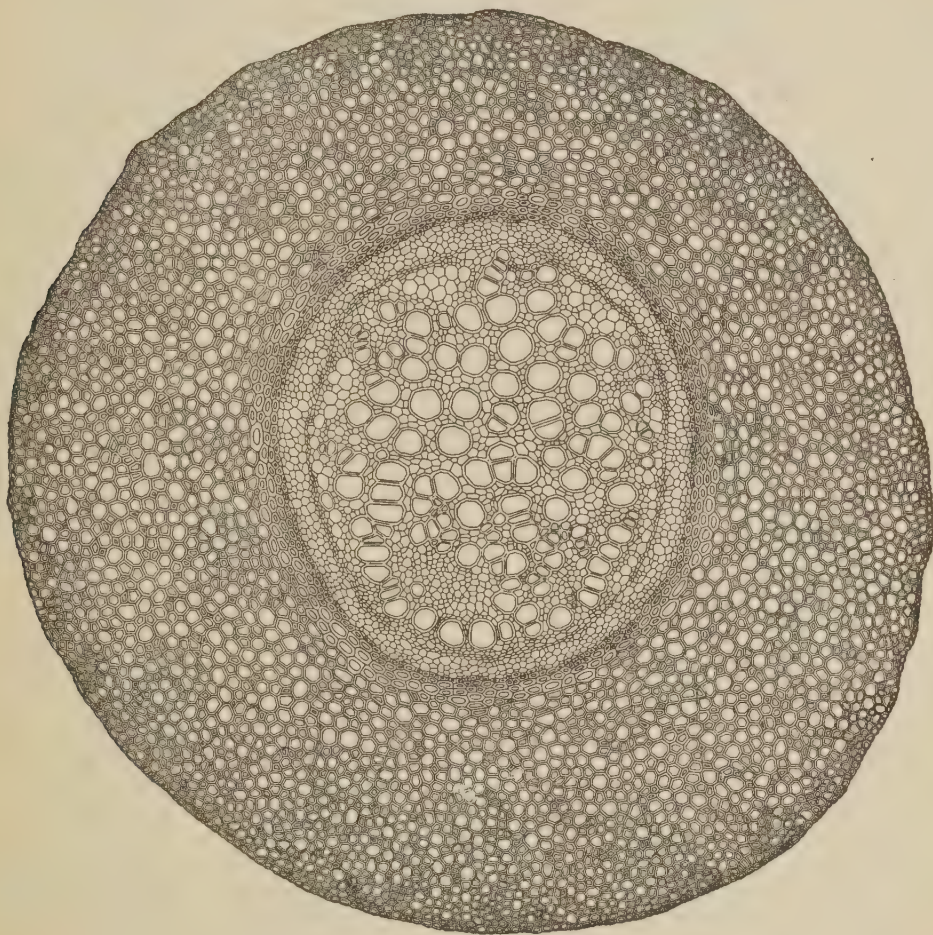


FIG. 426. Cross section of a fern stem (*Gleichenia*) showing protostele. Note that the stele is solid and is concentric, that is, the xylem is surrounded by the phloëm. Outside the stele is the cortex. ( $\times 50$ )

The structure and appearance also vary greatly in different cases. The sporophyte of typical ferns has a fair-sized stem, leaves (Fig. 424), and numerous roots.

The characteristic type of vascular bundle in the stems of ferns is *concentric* (Fig. 425), the xylem being surrounded by phloëm. The most primitive type of stele is a *protostele* (Fig. 426), or



solid stele, in which there is no pith within the vascular system. A more advanced type is the *siphonostele* (Fig. 427), in which the vascular system is in the form of a cylinder that incloses a central pith. Where a bundle that supplies a leaf leaves

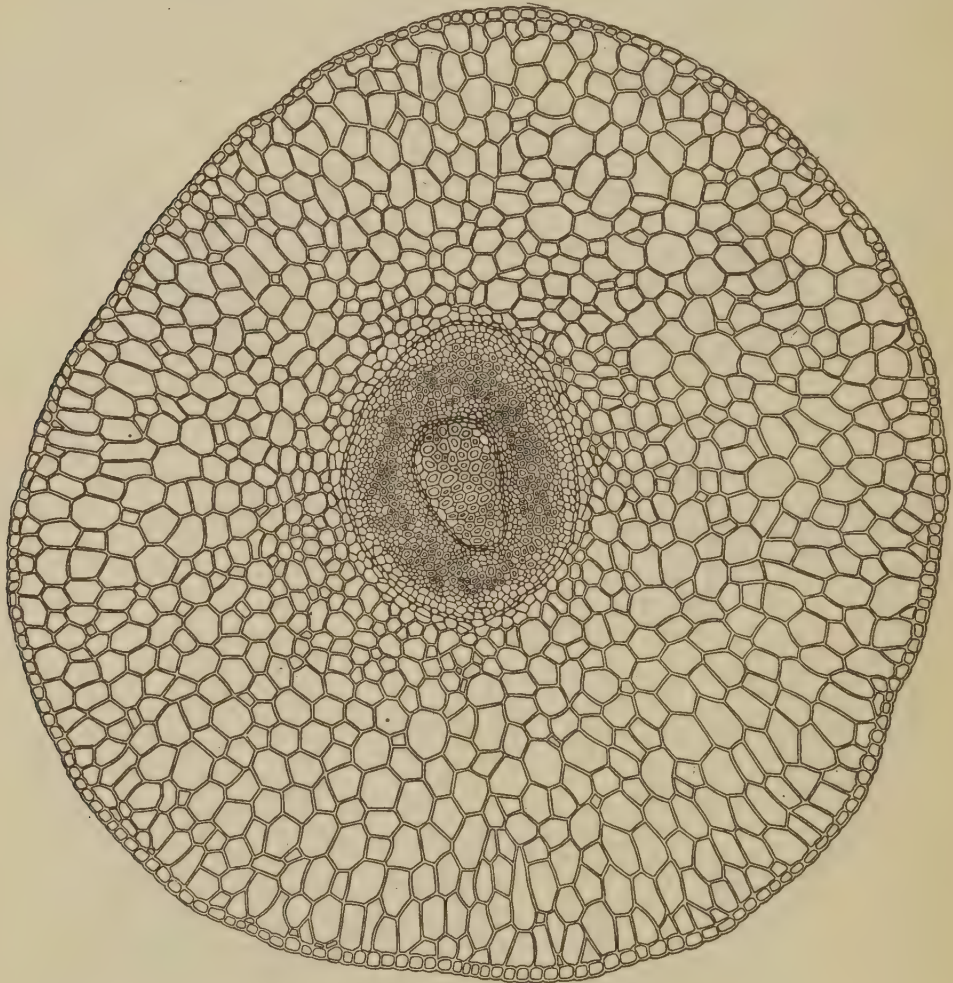


FIG. 427. Section of a stem of a maidenhair fern (*Adiantum*), showing a siphonostele

Note that there is a central pith composed largely of thick-walled sclerenchyma cells, and that outside the stele is a wide cortex. The xylem is bordered on both sides by phloem. ( $\times 35$ )

the siphonostele, an opening, or *leaf gap* (Fig. 428), occurs in the cylinder above the place of origin of the leaf bundle. When these gaps are greatly elongated and extend through several nodes, the cylinder consists of a coarse mesh, and in cross section the stele appears to be composed of a number of separate bundles (Fig. 429). Such a type of stele is merely a modification



of a simple siphonostele, but is frequently called a polystele and may be further complicated by the formation of extra bundles which develop as branches from the original cylinder.

In primitive siphonosteles the xylem is bordered by phloëm, both toward the center and toward the exterior (Fig. 427). In certain more advanced types there is no internal phloëm. The steles of modern conifers and dicotyledons appear to have been derived from a siphonostele from which the internal

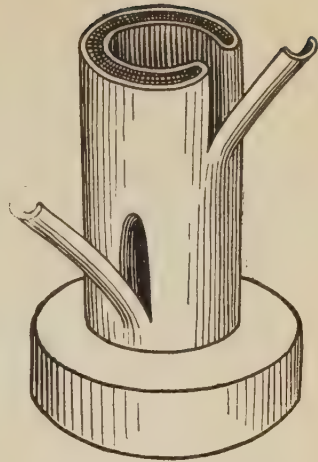


FIG. 428. Diagram of a siphonostele of a fern, showing leaf gaps where leaf traces leave the stele

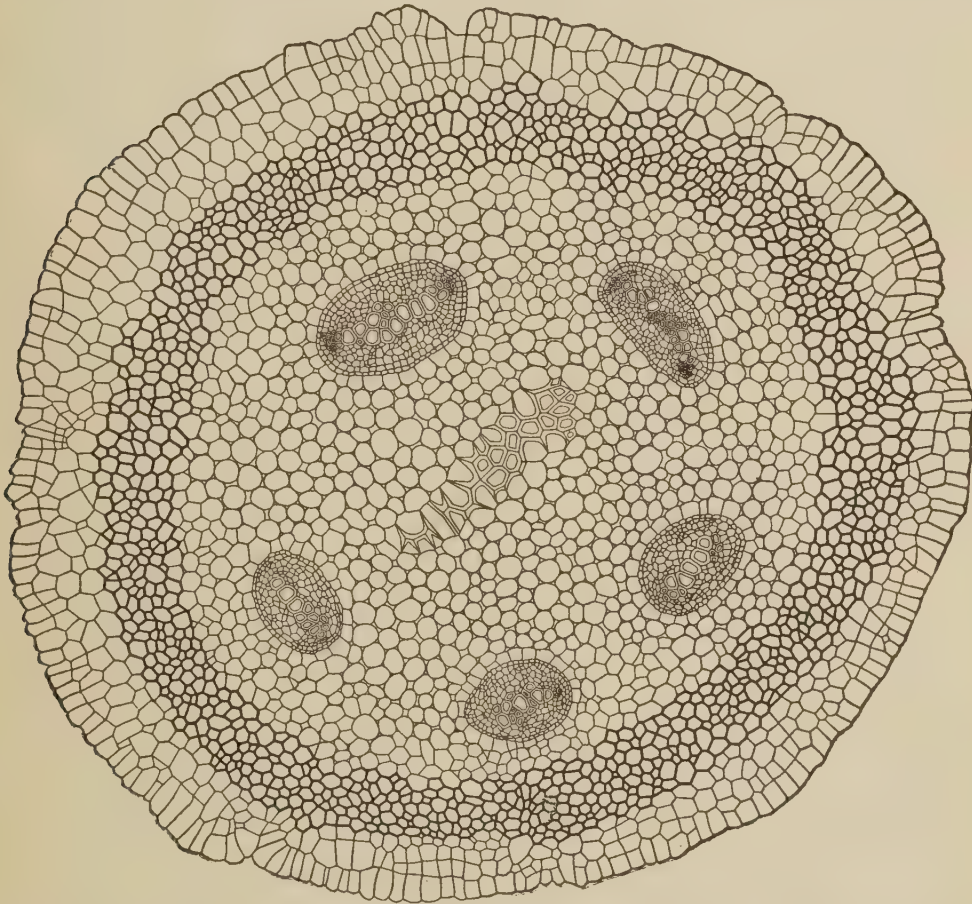


FIG. 429. Cross section of stele of a fern (*Cyclophorus adnascens*), in which leaf gaps are so long that there appear to be five separate bundles in the stele. Note the sclerenchyma in the center of the stele and also the cylinder of sclerenchyma near the outside of the cortex. ( $\times 50$ )

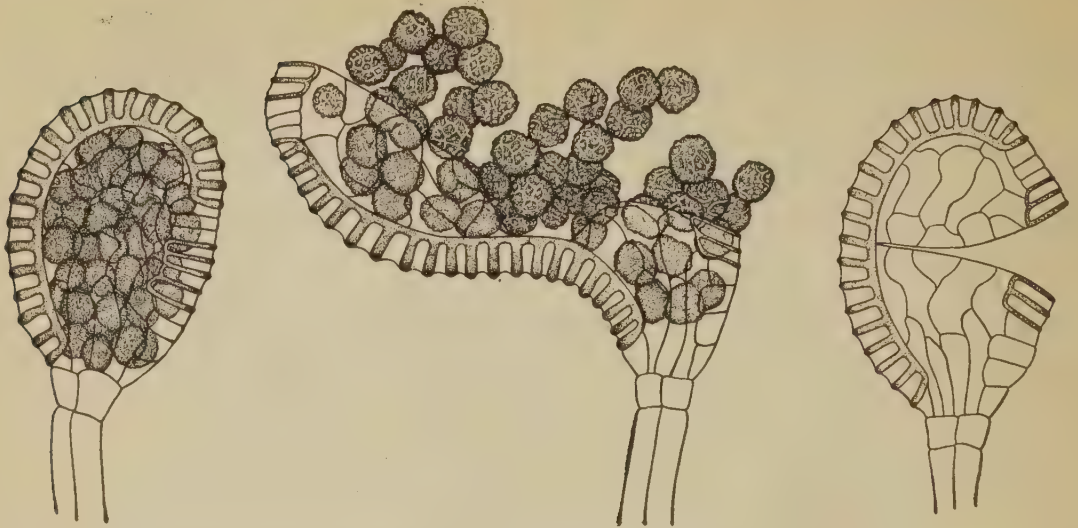


FIG. 430. Sporangia of a fern (*Pteris longifolia*)

Left, entire sporangium; center, sporangium opened by the bending back of the annulus (the row of thick-walled cells); right, an annulus has returned to its original position, which movement resulted in the scattering of the spores. ( $\times 85$ )

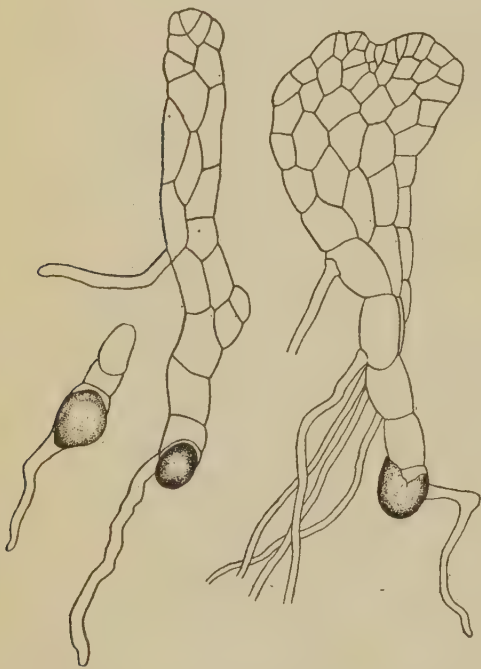


FIG. 431. Germination of fern spore and early stages in growth of prothalli

phloëm has disappeared and in which there has been a massive development of secondary xylem.

The sporangia of ferns are usually borne on the lower surfaces of the leaves (Fig. 424) and are aggregated in definite areas, the *sori*. In each sporangium there are many spores (Fig. 430). When a spore germinates, it produces a small green thallus, the gametophyte (Figs. 431, 432).

**Gametophyte.** The gametophyte of the *Pteridophyta* is known as the *prothallus* (Fig. 432). It is typically a delicate, thin, expanded thallus which is

attached to the ground by means of numerous rhizoids. The latter are slender filaments which absorb water and mineral matter just as do the root hairs of flowering plants. The typical prothallus is an independent plant which manufactures its food



by means of its chloroplastids and absorbs water through its rhizoids. Usually a prothallus bears both archegonia and antheridia (Fig. 432), but in some cases the antheridia and archegonia are borne on different prothalli. The *antheridia* (Figs. 432, 433) are spherical and contain numerous spermatozoids. The

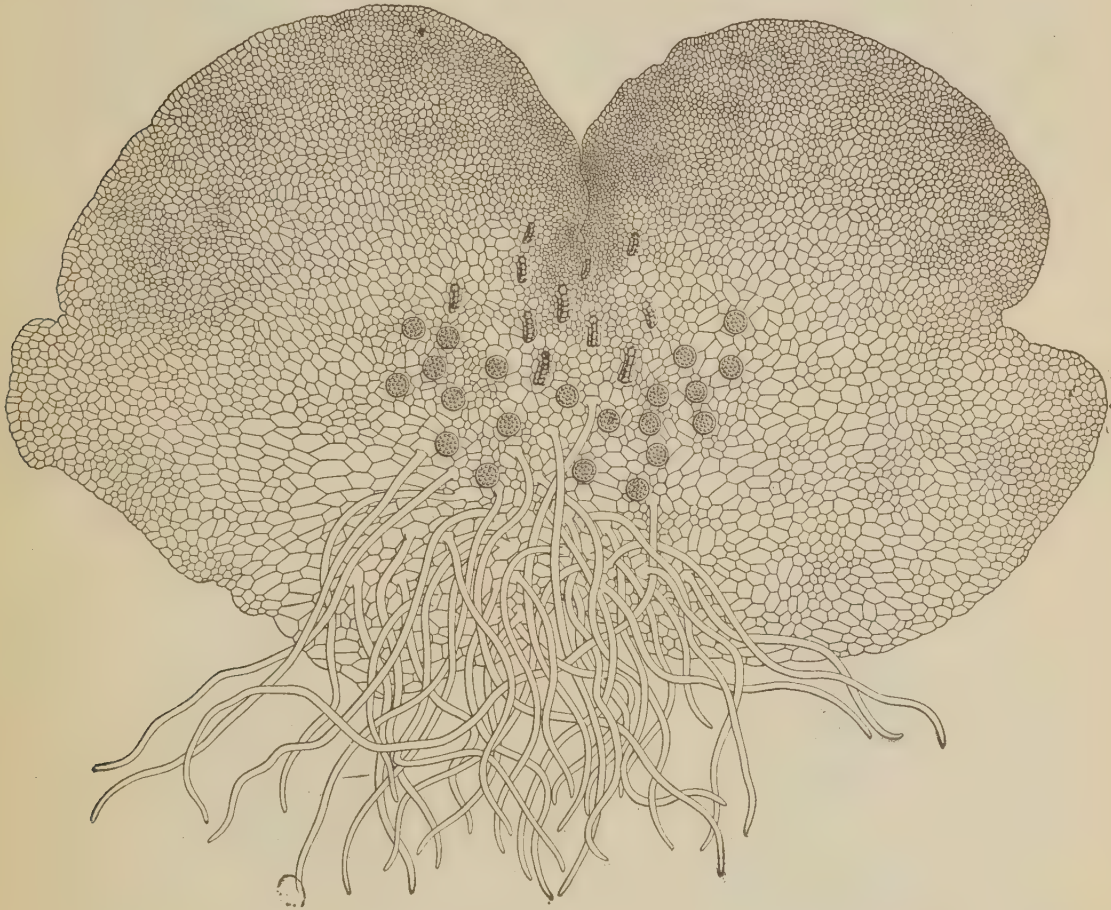


FIG. 432. Lower surface of prothallus, or gametophyte, of a fern

Near the base of the prothallus are numerous rhizoids; in the center are rounded antheridia containing spermatozoids; near the apex are archegonia which point toward the base

spermatozoid (Fig. 433) is a spiral structure, toward one end of which are numerous cilia which enable it to swim through water. As in the *Bryales*, an *archegonium* is a flask-shaped structure. In the enlarged basal portion, or venter, there is a large egg (Fig. 434), and above this a smaller cell, the ventral-canal cell. In the neck of typical ferns there are two neck-canal cells. When the archegonium matures, the ventral-canal cell and



FIG. 433. Antheridium of a fern

Left, an antheridium on the side of a prothallus of a fern; note the coiled spermatozooids within the antheridium ( $\times 845$ ). Right, a single spermatozoid of a fern. (Spermatozoid redrawn after Yamanouchi)

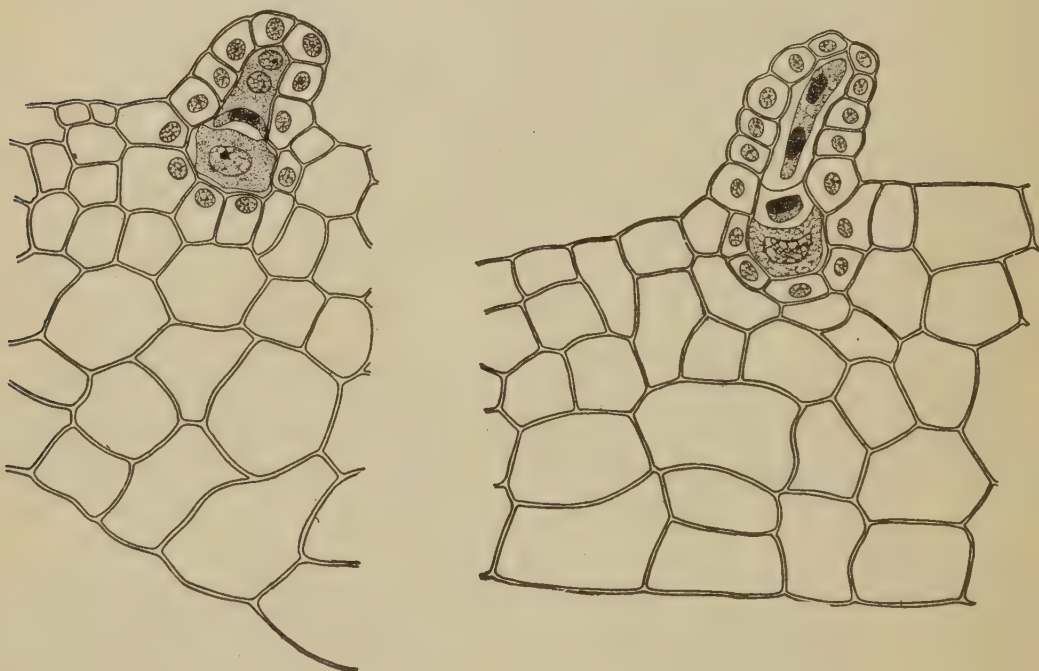


FIG. 434. Archegonia of a fern

Left, the enlarged base, or venter, contains an egg and above this is the ventral canal cell, while in the neck are two neck canal cells; right, the ventral canal cell and neck canal cells have begun to disorganize. ( $\times 185$ )





FIG. 435. Archegonia of a fern

Left, the neck-canal cells and ventral-canal cell are disorganized, but the archegonium has not opened ; right, archegonium open. (Redrawn after Strasburger)



FIG. 436. Prothallus of a fern with young sporophyte attached

Left, as seen from above ; right, as seen from below. ( $\times 3\frac{1}{2}$ )

neck-canal cells become disorganized (Figs. 434, 435) and the tip of the archegonium opens (Fig. 435), so that there is a passage through which the sperm can reach the egg. The rounded basal part of the archegonium is sunk within the prothallus, while

the neck projects from the surface of the prothallus. Fertilization takes place when a spermatozoid swims from an antheridium, enters an archegonium (Fig. 437), and fuses with the egg

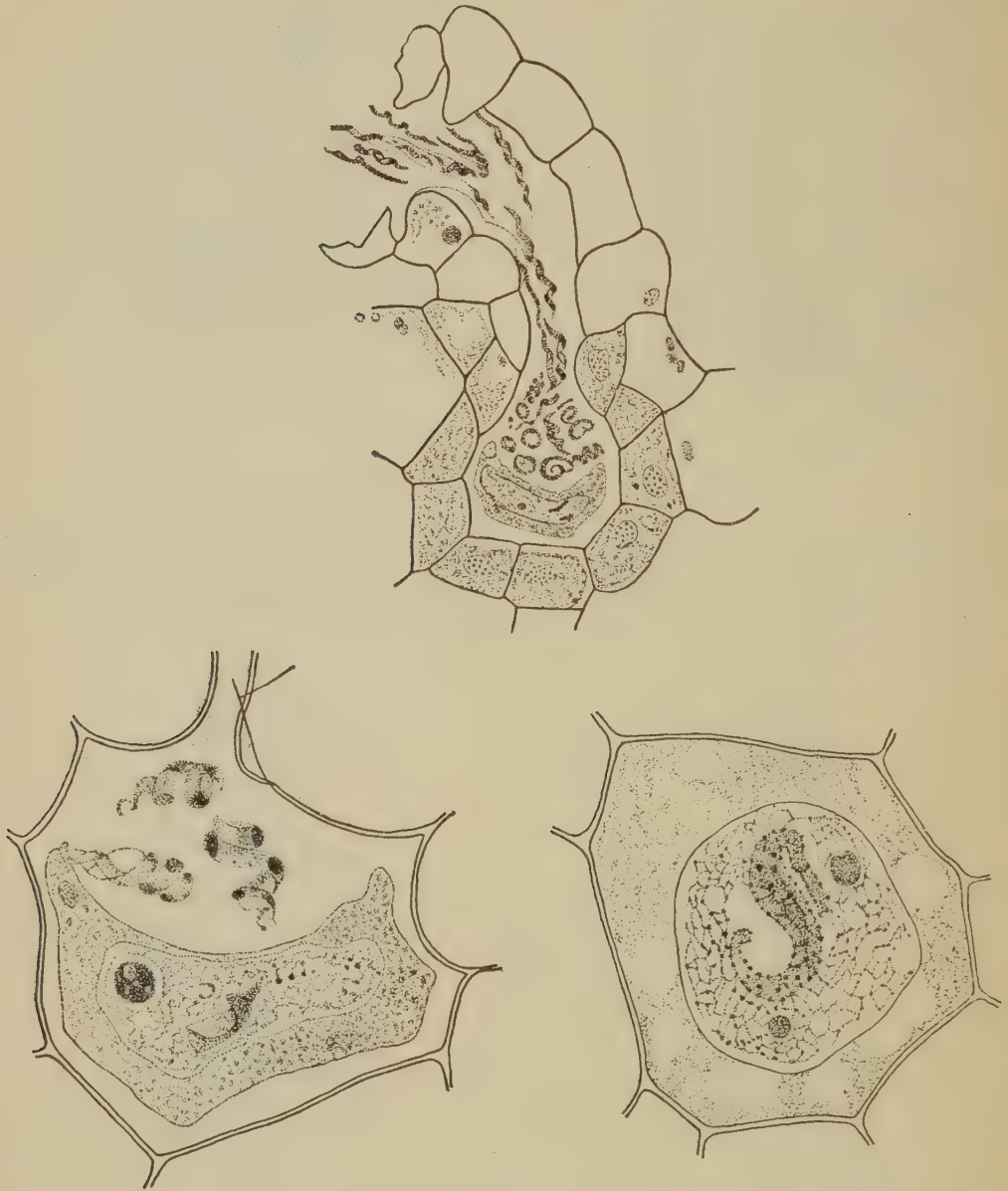


FIG. 437. Fertilization in a fern

Above, spermatozoids are entering neck of archegonium; lower left, vertical section through venter, showing a single spermatozoid in the nucleus of the egg; lower right, horizontal section through venter, showing a later stage in the union of spermatozoid and egg nucleus. (Redrawn after Shaw)

(Fig. 437). As in the case of the *Bryales*, water is necessary to accomplish fertilization, because the spermatozoid has no way of reaching the archegonium except by swimming.



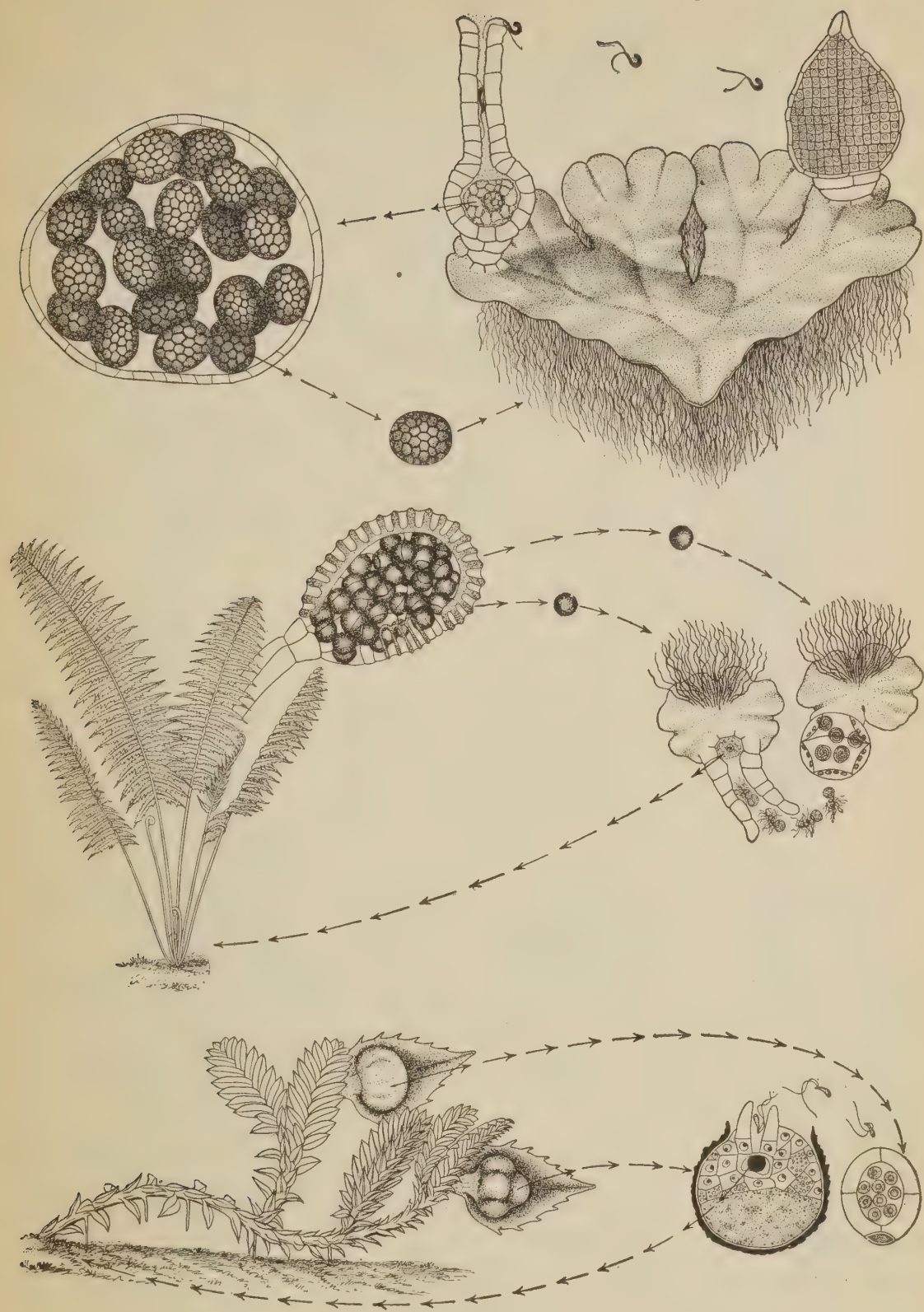


FIG. 438. Diagram of alternation of generations in *Bryophyta* and *Pteridophyta*  
 Above, *Riccia*; center, a fern; below, *Selaginella*

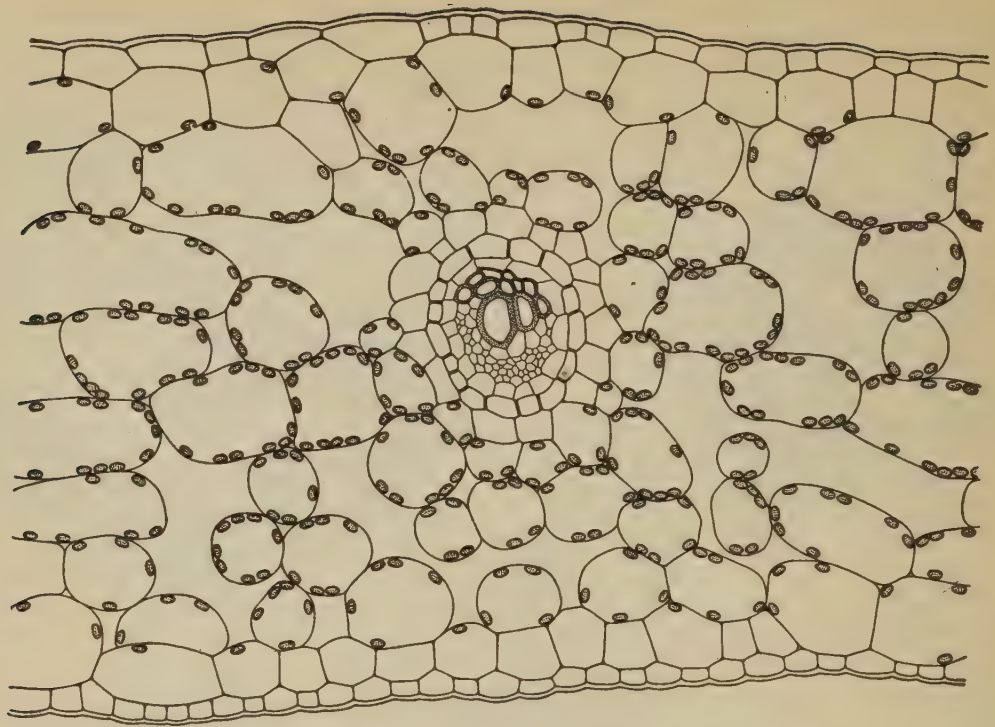


FIG. 439. Cross section of a fern leaf. ( $\times 240$ )



FIG. 440. *Equisetum arvense*

Left, sporophyte with fertile branch (at the right) and two young sterile branches (at the left) ( $\times \frac{1}{2}$ ); center, shield-shaped sporophyll with sporangia ( $\times 10$ ); right, sterile branch ( $\times \frac{1}{3}$ )



**Development of sporophyte.** The fertilized egg develops at once into a sporophyte (Fig. 436). During the early stages of its growth the sporophyte is dependent on the prothallus

for nourishment. The fertilized egg divides into four segments, one of which develops into a foot, which absorbs nourishment from the prothallus. The

young embryo, however, soon produces a stem, roots, and leaves, and thus becomes independent of the gametophyte.

After such development has occurred, the gametophyte dies and the sporophyte continues to live independently.

Thus, in a typical fern (Fig. 438) the sporophyte and the gametophyte are independent plants.



FIG. 441. Tip of a branch of *Equisetum hiemale* ending in a strobilus. ( $\times 1$ )

**Alternation of generations.** As in the *Bryophyta*, the cells of the gametophyte contain an  $x$ , or single, number of chromosomes, and those of the sporophyte a  $2x$ , or double, number. Again, as in the *Bryophyta*, the spores are formed in tetrads (groups of four) by two successive divisions of each spore mother cell. The reduction in the number of chromosomes occurs in the first of these two divisions. The double number is restored when an egg is fertilized by a spermatozoid. Therefore the ferns resemble the bryophytes in having an alternation of generations, consisting of a gametophyte with an  $x$  number of chromosomes and a sporophyte with a  $2x$  number.



FIG. 442. *Lycopodium reflexum*, with sporophylls scattered over the stem. ( $\times \frac{1}{2}$ )

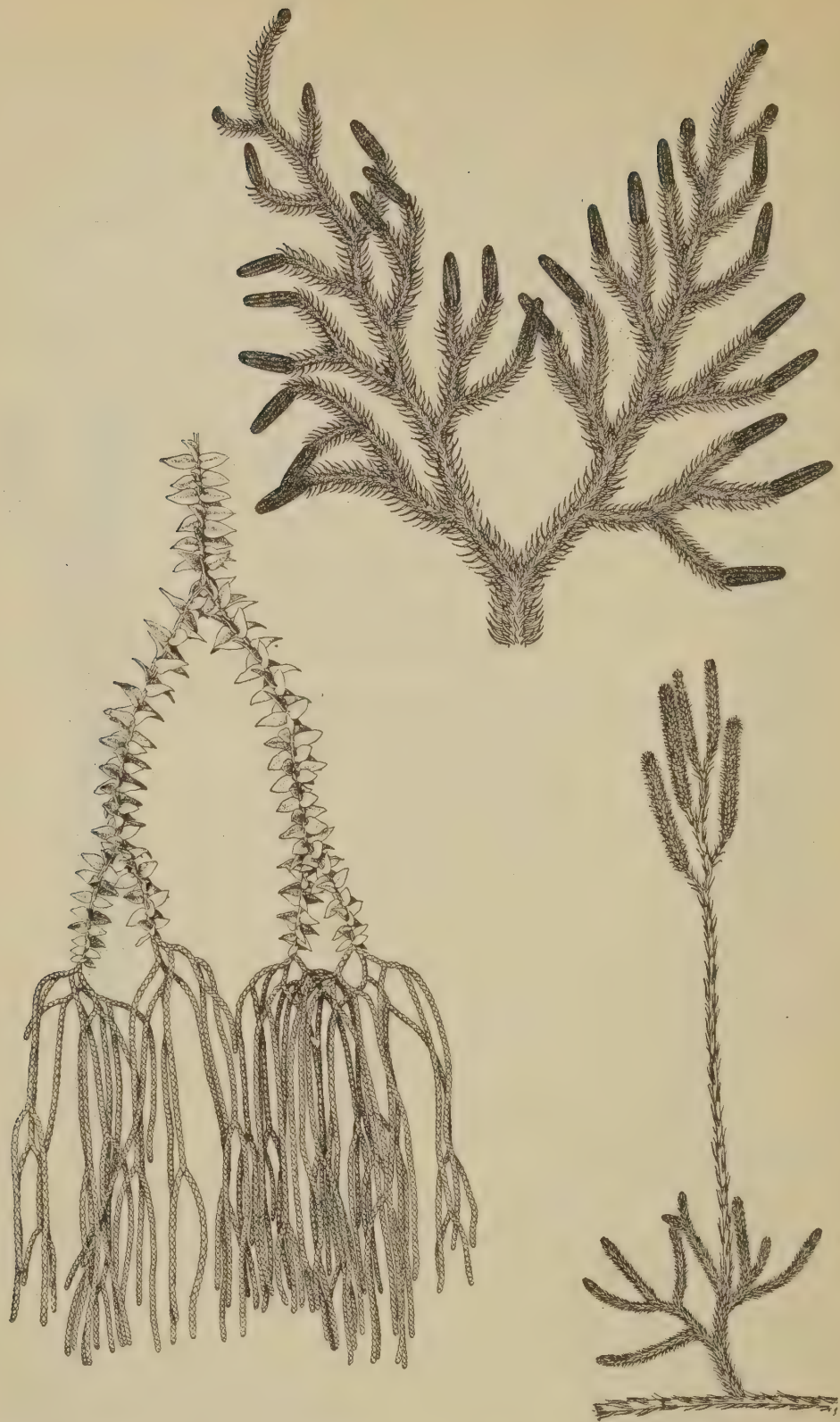


FIG. 443. Portions of sporophytes of *Lycopodium* with sporophylls aggregated into terminal strobili

Above, a terrestrial tropical species (*Lycopodium cernuum*) ( $\times \frac{2}{3}$ ); lower left, an epiphytic tropical species (*Lycopodium phlegmaria*) ( $\times \frac{1}{4}$ ); lower right, a terrestrial species (*Lycopodium clavatum*) found in the temperate zone and on tropical mountains ( $\times \frac{1}{3}$ )



**Relationship of ferns.** In possessing an alternation of sporophyte and gametophyte generations the ferns resemble the liverworts very closely. Moreover, the thallus of a fern is very similar



FIG. 444. A single sporophyll of *Lycopodium*, with sporangium on the upper surface near the base. ( $\times 5$ )

to that of some of the simple liverworts. The greatest difference between the liverworts and the ferns lies in the development of the sporophytes. In some of the simple liverworts the sporophyte consists of only a single sporangium without a stalk, while in the majority it lacks chlorophyll and is composed of a sporangium, a stalk, and an absorbing organ, the foot. In both of these cases the sporophyte is entirely dependent on the gametophyte for nourishment. In the highest order of the liverworts, the *Anthocerotales*, the sporophyte is more complex. In *Anthoceros* it has stomata of the type found in higher plants and a considerable development of assimilating tissue containing chloroplasts. It thus manufactures food instead

of being entirely dependent on the gametophyte, as in the simple liverworts. In the ferns the sporophyte is much more highly specialized than in any of the liverworts. In the first stages of its growth the sporophyte of a fern develops a foot and is dependent on the gametophyte for nourishment; but it soon produces a stem, roots, and leaves and becomes

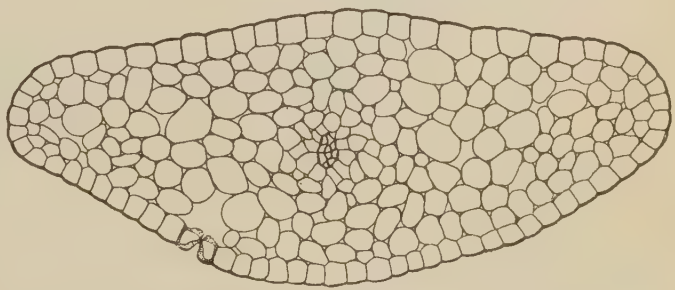


FIG. 445. Cross section of a leaf of *Lycopodium*. ( $\times 105$ )

independent. In all the liverworts the gametophyte is the dominant stage in the life history. In the ferns the sporophyte, and not the gametophyte, is the dominant stage.

A relationship between the liverworts and ferns is indicated by the facts that in both the groups there is an alternation of a gametophyte and a sporophyte generation and that the gametophytes are very similar in both cases.

CLASS *EQUISETINEAE* (HORSETAILS)

This is a small class of plants containing the single genus *Equisetum*. *Equisetum*, like all other pteridophytes, shows an

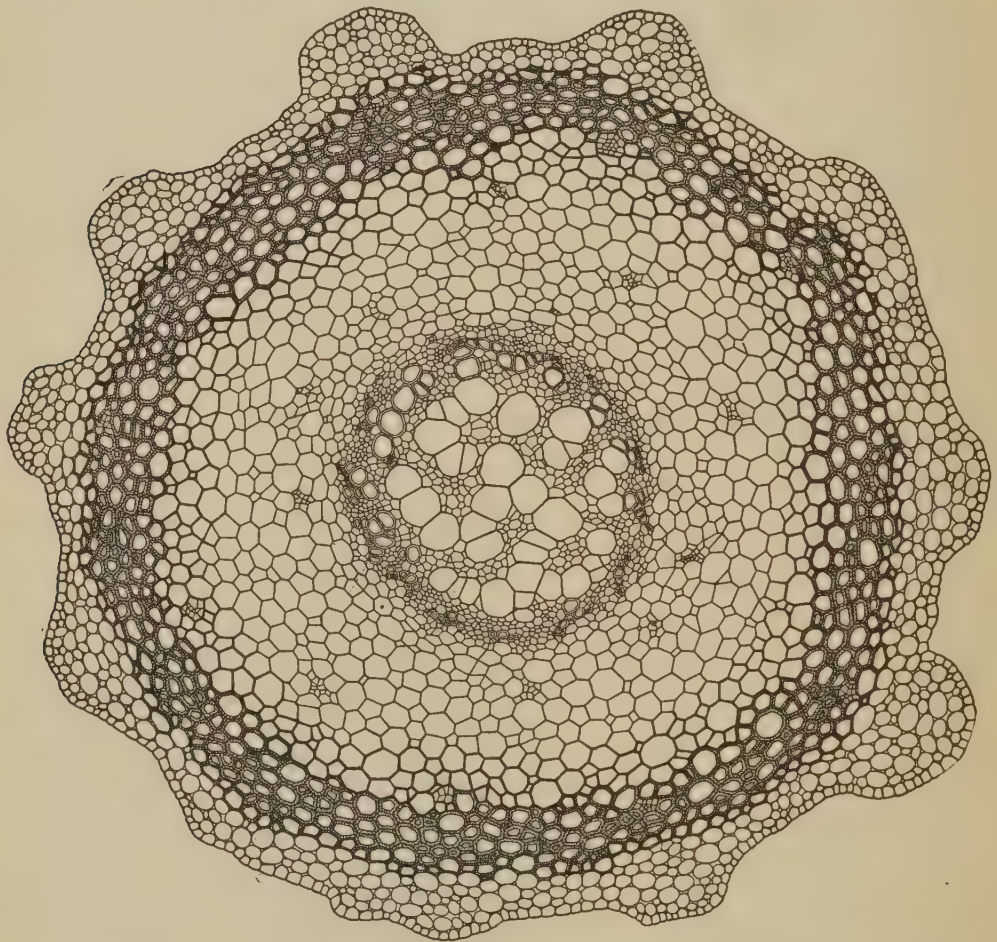


FIG. 446. Cross section of a stem of *Lycopodium cernuum*, showing radial protosteles in which phloem occurs between the strands of xylem

Note the sclerenchyma cells near the outer part of the cortex. ( $\times 45$ )

alternation of a sporophytic and a gametophytic generation. The gametophyte is a simple thallus bearing archegonia or antheridia. The sporophyte consists of an underground rhizome (Fig. 440) which produces hollow, erect, aërial stalks. The leaves are



scalelike and borne in whorls (Figs. 440, 441). The sporangia are found on specialized leaves (sporophylls) which occur in terminal strobili, — conelike aggregations of sporophylls (Figs. 440, 441). This class of plants is unimportant in our present flora, but in past geologic ages it was represented by numerous large trees. These were important constituents of the forests of the Carboniferous period.

#### CLASS LYCOPODINEAE (CLUB MOSSES)

The most important orders of the *Lycopodineae* are the *Lycopodiales* and the *Selaginellales*. The class *Lycopodineae* is an unimportant constituent of our present flora, but, like the *Equisetinae*, was represented in the Carboniferous Age by large trees which were prominent constituents of the forests.

#### ORDER LYCOPODIALES

*Lycopodium*. The genus *Lycopodium* is by far the commonest and most widespread in this order. In all the species the sporophyte is a small plant, the stems of which are more or less thickly covered with small, pointed leaves (Figs. 442, 443). The sporangia are borne singly on the upper surface near the base of a leaf (Fig. 444). The *sporophylls* (leaves with sporangia) may resemble the ordinary leaves and be scattered over the stem (Fig. 442), or they may be somewhat different in shape and be aggregated in terminal strobili (Fig. 443). The gametophyte is a small thallus.



FIG. 447. Portion of a plant of *Selaginella* with sporophylls aggregated in terminal strobili. ( $\times 1$ )

ORDER *SELAGINELLALES*

*Selaginella*. This genus is the only representative of the order *Selaginellales*. The sporophyte is a small, fernlike plant with small, scalelike leaves (Fig. 447). Some of the species are cultivated for ornamental purposes. The sporangia are borne singly

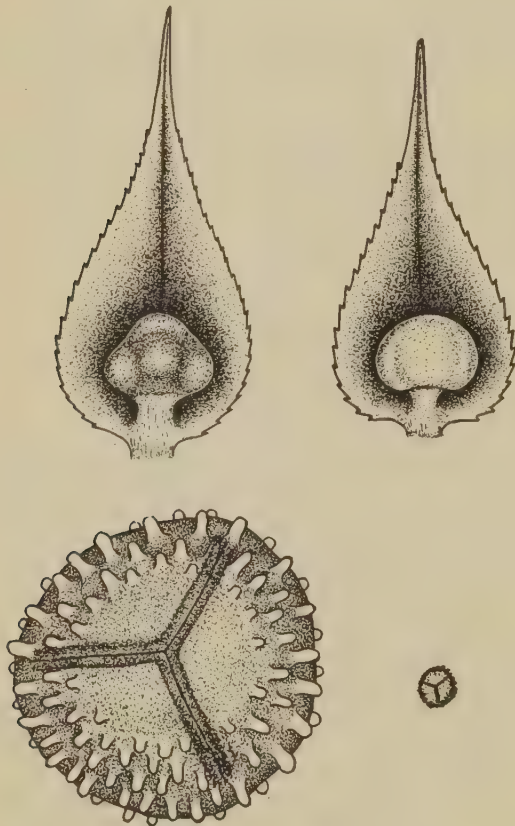


FIG. 448. Sporangia and spores of *Selaginella*. Upper left, megasporophyll with megasporangium containing four megaspores ( $\times 15$ ); upper right, microsporophyll ( $\times 15$ ); lower left, megaspore ( $\times 75$ ); lower right, microspore ( $\times 75$ ).

on the upper surface near the base of the sporophylls. In some species the sporophylls are similar to ordinary leaves, but in most cases they are smaller and aggregated into terminal strobili (Fig. 447). The sporangia are of two kinds (Fig. 448), *microsporangia* and *megasporangia*, and the sporophylls which bear them are called, respectively, *microsporophylls* and *megasporophylls*. A microsporangium contains numerous small spores, *microspores*, while each megasporangium contains four large spores, *megaspores*. The microspores give rise to male prothalli, and the megaspores to female prothalli. The *male prothallus* develops within the spore wall and consists of a single prothallial cell and an antheridium (Fig. 449). The *female prothallus* also begins to develop within the spore wall. As the prothallus continues to develop, the spore wall is burst and the apex of the prothallus with the archegonia is exposed (Fig. 449). The egg is fertilized by a motile



spermatozoid, and the fertilized egg develops into a sporophyte, as in other pteridophytes. In some cases archegonia may be produced, the eggs may be fertilized, and sporophytes may begin to develop before the spores are shed.

**Specialization of sporangia.** The sporangia of *Selaginella* show greater specialization than do those of typical ferns in that they

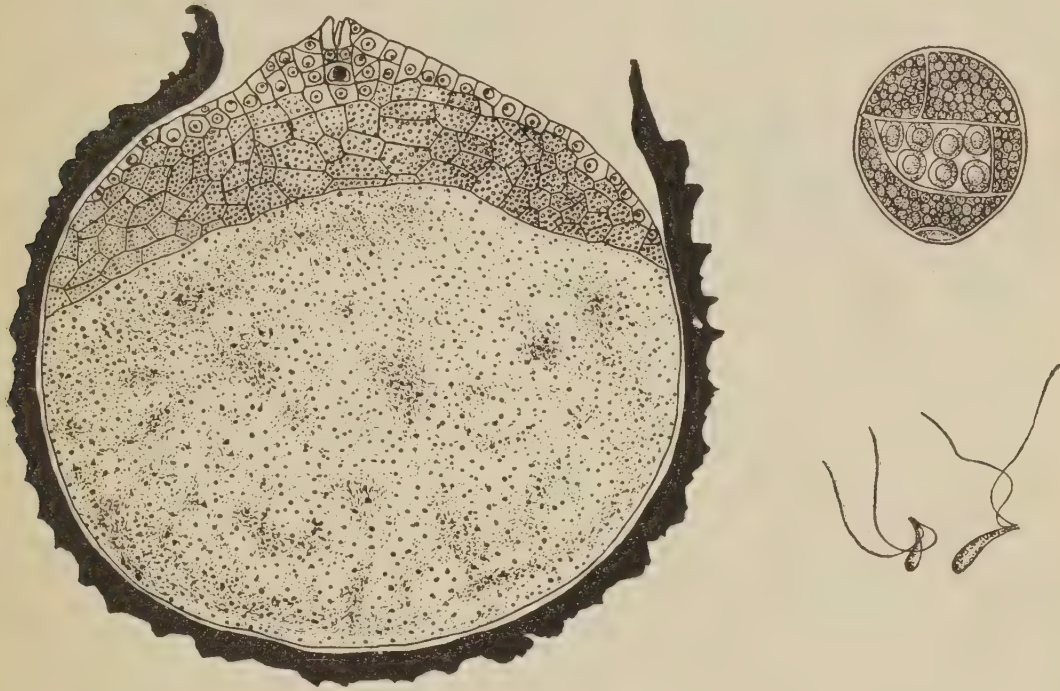


FIG. 449. Gametophytes of *Selaginella*

Left, section of a female prothallus; the megaspore wall is shown in black; note the archegonium projecting from the upper surface of the prothallus (redrawn after Miss Lyons). Upper right, male gametophyte of *Selaginella*; note that it consists of a single prothallial cell and a single antheridium (redrawn after Belajeff).

Lower right, spermatozooids of *Selaginella* (redrawn after Belajeff)

are differentiated into megasporangia and microsporangia. The differentiation of the sporangia and spores of *Selaginella* has been accompanied by a decrease in size and a loss of independence in the prothalli. They are small and are dependent for development on food stored by the sporophyte in the spore.

The differentiation of spores into megaspores and microspores, and their dependence on the sporophyte, has certain obvious advantages. The delicate prothalli of ferns do not appear to be very well suited to life on dry land, as they require a considerable

period of favorable moist conditions for their development. The sporophyte of a fern, on account of its structure, can withstand conditions that would be fatal to the prothallus. As the gametophytes of *Selaginella* derive their nourishment from the sporophyte, they are more independent of external conditions than are those of ferns.

A differentiation of spores into megaspores and microspores has occurred in several lines of pteridophytes. This differentiation

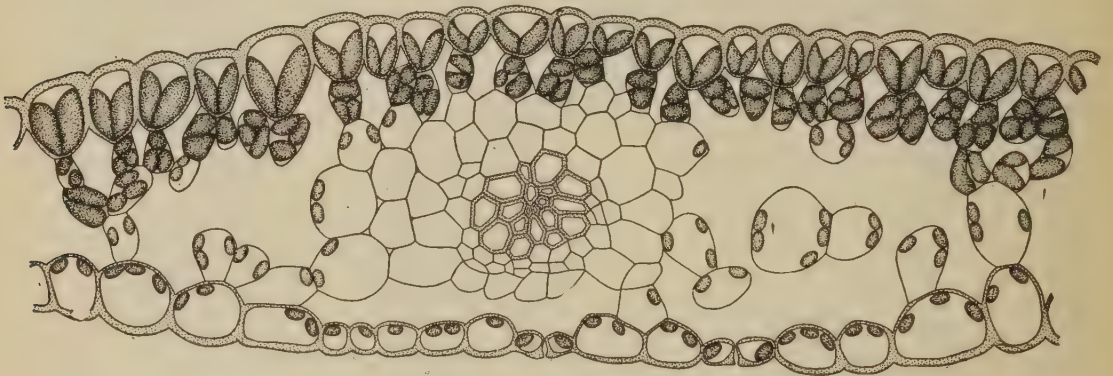


FIG. 450. Cross section of a portion of a *Selaginella* leaf. ( $\times 235$ )

is found in the peculiar water ferns, and it appears that a similar differentiation in ferns, in a past geologic age, led to the development of modern seed plants.

It is of interest to compare the gametophytes and sporophytes of liverworts, ferns, and *Selaginella* (Fig. 438). In all but the most advanced types of liverworts the sporophyte is entirely dependent on the gametophyte for nourishment. Even in *Anthoceros* the sporophyte is partially dependent on the gametophyte. In typical ferns the gametophyte and sporophyte are both independent plants. In *Selaginella* the gametophyte is dependent on the sporophyte for nourishment, the reverse of the condition in liverworts.

**Interrelationship of *Pteridophyta*.** The relationship between the *Filicineae*, the *Equisetineae*, and the *Lycopodineae* is a much-disputed question. Certainly no one of these classes seems to have been derived from a modern representative of another. It would appear, however, that all three are descended from a common ancestor.



## CHAPTER XIII

### DIVISION SPERMATOPHYTA

The spermatophytes include all the seed-bearing plants. This is the most important division in the vegetable kingdom and contains the dominant plants of our present flora.

In the spermatophytes, as in the pteridophytes, there is an alternation of generations, the conspicuous generation being the sporophyte. The reproductive cells that are produced by the sporophyte are *megaspores* (Fig. 463) and *microspores*. The megaspores are formed in megasporangia called ovules, while the microspores, or pollen grains, are found in microsporangia known as pollen sacs (Figs. 206, 481).

Considerable confusion will be avoided by remembering that the word *ovule* is used to designate the particular kind of *megasporangium* characteristic of the spermatophytes.

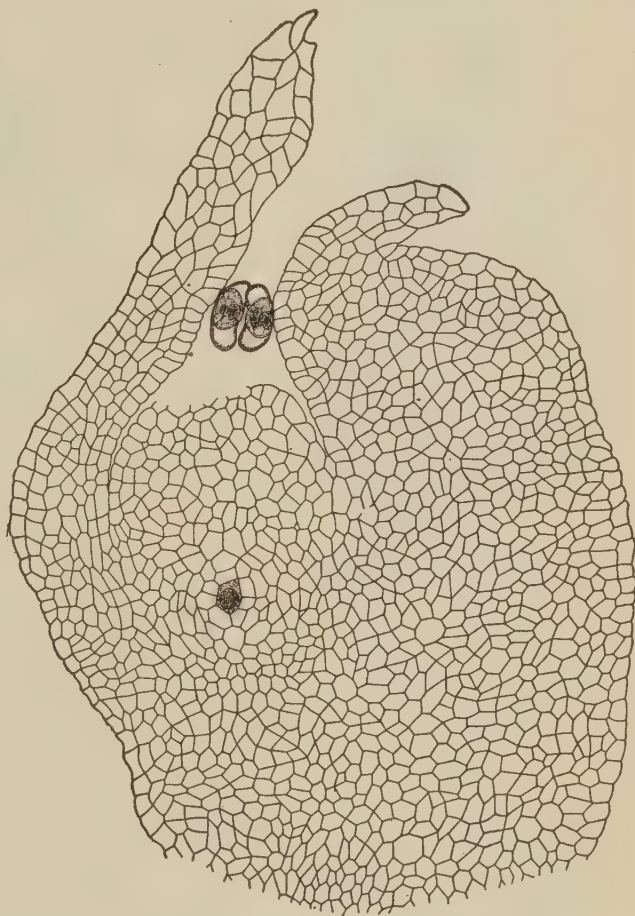


FIG. 451. Longitudinal section of megasporangium of pine

The megasporangium consists of the nucellus surrounded by an integument. The nucellus is free from the integument only near the apex; within the nucellus is the megaspore mother cell, the contents of which are shaded. In the opening (micropyle) there are two microspores containing male prothalli. ( $\times 100$ )

Likewise, the term *pollen sac* is simply another name for the *microsporangium* of the spermatophytes, while a *pollen grain* is a *microspore* of a spermatophyte. The spermatophytes are divided into the two groups *gymnosperms* and *angiosperms*. In the angiosperms the megasporangia are inclosed in ovaries, while in the gymnosperms they are exposed as in the pteridophytes.

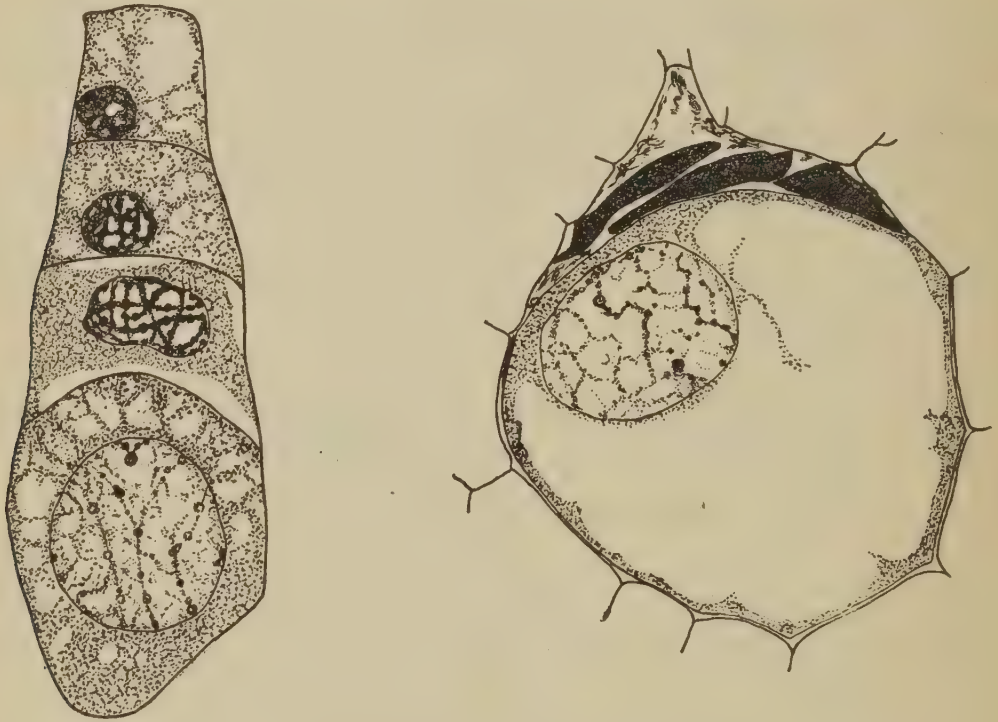


FIG. 452. Megaspores of pine

Left, row of four megaspores of pine ; the basal one will give rise to the female prothallus. Right, three apical megaspores are disorganizing, while the basal one has enlarged considerably. (Redrawn after Miss Ferguson)

**Megasporangium and female gametophyte.** The megasporangium (ovule) consists of a central mass, the *nucellus*, or sporangium proper, inclosed in one (Fig. 451) or two envelopes called *integuments*. The integuments arise as collarlike outgrowths which grow up over the nucellus and inclose it completely except at the apex, where there is a small opening, the *micropyle*. A *megaspore mother cell* is formed within the nucellus (Fig. 451). In most species there is only one megaspore mother cell, but in some cases there are more. Typically the megaspore mother cell divides to form a row of four *megaspores* (Fig. 452). Three of these



degenerate, while the remaining one germinates (Fig. 452) and produces a *female gametophyte*, or *prothallus*, which remains per-

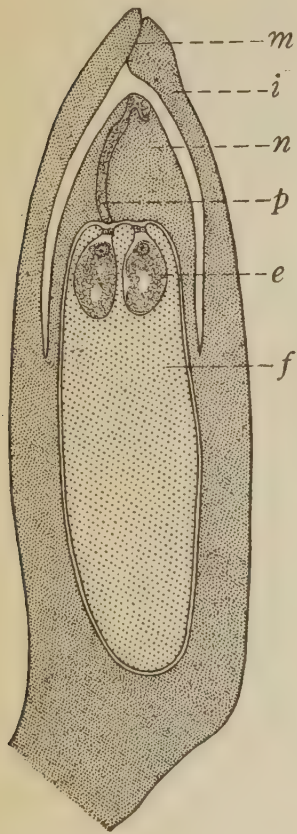


FIG. 453. Somewhat diagrammatic longitudinal section of megasporangium of pine, containing a female prothallus with two archegonia

*m*, micropyle; *i*, integument; *n*, nucellus; *p*, pollen tube; *e*, egg in archegonium; *f*, female prothallus. ( $\times 14$ )

manently inclosed within the sporangium (Fig. 453). In most of the gymnosperms archegonia are produced at the micropylar end of the prothallus, but in the angiosperms there are no archegonia and one of the cells of the prothallus becomes an egg.

**Microsporangia and microspores.** The microspores (pollen grains) are borne in microsporangia on microsporophylls (Figs. 206, 481), which in the angiosperms are called stamens. In the gymnosperms the microspores are carried by the wind, and by chance some are deposited at or in the micropyle (Fig. 451)

of a megasporangium (ovule). The microspore sends out a pollen tube that grows through the nucellus toward the archegonia (Fig. 453). The eggs in the archegonia are fertilized either by spermatozoids or by male

nuclei from the pollen tube. In the angiosperms, where the megasporangia (ovules) are inclosed in an ovary, the microspores are deposited on the stigma, and the pollen tube grows through the style before reaching the megasporangium (Fig. 4).

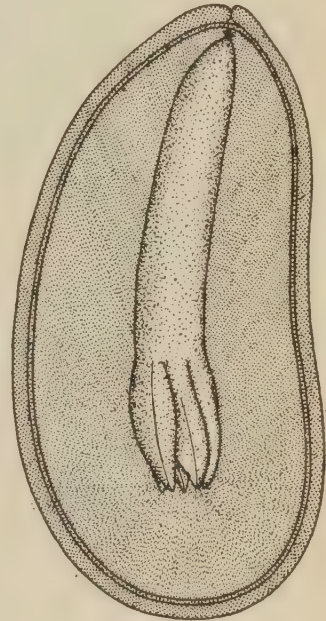


FIG. 454. Longitudinal section of pine seed consisting of the embryo surrounded by the female prothallus and this in turn by the seed coat formed from the integument. ( $\times 5$ )



FIG. 455. *Cycas rumphii*

At the apex there is a group of young megasporophylls with megasporangia slightly past the pollination stage; below the sporophylls is a whorl of foliage leaves; below this is a circle of old sporophylls with nearly matured seeds; below these sporophylls is another whorl of leaves. ( $\times \frac{1}{8}$ )

**Seed.** The fertilized egg germinates and produces an embryo which is inclosed within the tissue of the megasporangium. The embryo, together with the surrounding tissue of the female



gametophyte and of the megasporangium (Fig. 454), or of the megasporangium alone, is known as a seed. The seed is the characteristic structure of the division *Spermatophyta*. Usually the nucellus almost completely disappears during the growth of the seed.

#### CLASS GYMNOSPERMAE

The class *Gymnospermae* is the more primitive of the two classes of the *Spermatophyta* and is characterized by megasporangia which are not inclosed in ovaries. It includes four orders, three of which are treated below.

#### ORDER CYCADALES

The cycads are a small group of plants with either a columnar (Fig. 455) or a tuberous stem which bears a crown of leathery, pinnately compound leaves. In the stem there is a relatively large pith surrounded by a band of woody tissue which increases in width



FIG. 456. Cross section of trunk of *Cycas chamberlainii*

by secondary thickening (Fig. 456). A slight development of secondary thickening is found in some ferns, but the cycads are the most primitive living plants that have a great development of secondary wood.

Both the *megasporangia* (ovules) and the *microsporangia* are borne on modified leaves known, respectively, as *megasporophylls* (Fig. 457) and *microsporophylls* (Fig. 458). The microsporophylls are relatively small, bear large numbers of sporangia on their lower surfaces, and are aggregated into definite cones (Figs. 459, 460) produced at the apex of the stem. In all the genera except

*Cycas* the megasporangia also occur in a cone (Fig. 462) at the apex of the stem. In the genus *Cycas* the megasporophylls are not in cones (Fig. 455) and are somewhat similar to ordinary leaves (Fig. 457). They are produced at the tip of the stem in whorls alternating with whorls of ordinary leaves (Fig. 455). The megasporophylls of *Cycas revoluta* are very leaflike in appearance

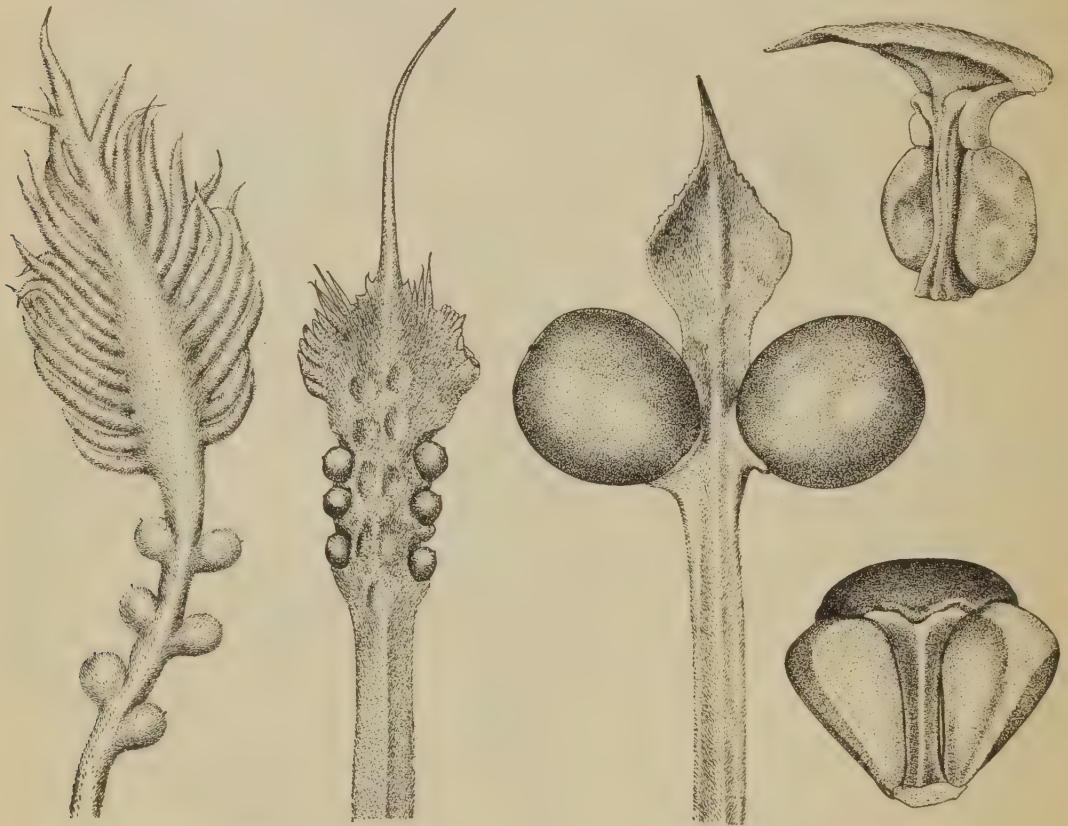


FIG. 457. Megasporephylls of cycads

Left, *Cycas revoluta* with young ovules ( $\times \frac{2}{5}$ ); second figure, *Cycas circinalis* with young ovules ( $\times \frac{2}{5}$ ); third figure, *Cycas rumphii* with seed ( $\times \frac{2}{5}$ ). This species usually bears six ovules, but two or four are also frequent. Upper right, *Dioon edule* with seed ( $\times \frac{2}{5}$ ); lower right, *Zamia* with seed ( $\times \frac{4}{5}$ )

(Fig. 457), while those of the genus *Zamia* bear almost no resemblance to ordinary leaves (Fig. 457). Between these two extremes there are various gradations (Fig. 457). The leaflike appearance of the megasporephylls of *Cycas revoluta* indicates that they have been derived from ordinary spore-bearing leaves, while the gradations between the megasporephylls of *Cycas revoluta* and those of *Zamia* indicate that even the highly modified sporophylls of *Zamia* had a similar origin.



**Megasporangium and female prothallus.** In the cycads the megasporangium consists of the nucellus and a single integument inclosing the nucellus, except that at the apex there is a small opening, the micropyle (Fig. 461). Within the megasporangium there is produced a megaspore mother cell which divides to form a row of three or four megaspores (Fig. 463). All except one of these degenerate and disappear,



FIG. 458. Under surface of microsporophyll of *Cycas rumphii*, showing many microsporangia. ( $\times 1\frac{1}{3}$ )

while the functional megaspore germinates within the megasporangium (Fig. 461) and produces a large, oval female prothallus (Fig. 464). This prothallus is retained permanently within the megasporangium. As the prothallus matures, it produces archegonia, which are usually in a group below the micropyle (Fig. 464). The archegonium of the cycads consists of two neck cells and a large egg cell (Fig. 465). The neck-canal cells found in bryophytes and pteridophytes are lacking, while the ventral-canal cell is represented by an evanescent nucleus which, with the surrounding cytoplasm, disorganizes soon after its formation (Fig. 466). This evanescent nucleus appears to have no function, but represents the survival of an ancestral characteristic.

**Male prothallus and fertilization.** Before being shed the microspore (pollen grain) germinates and produces a male gametophyte, or prothallus, within the microspore (Fig. 468). This gametophyte consists of a sterile prothallial cell, a generative cell, and a tube cell. In this three-celled condition

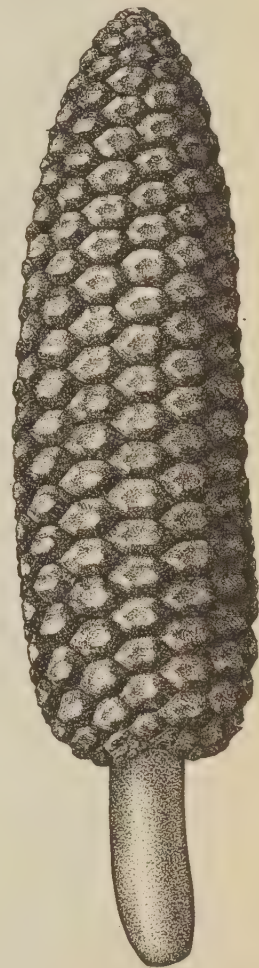


FIG. 459. Cone of microsporophylls of *Zamia floridana*. ( $\times 1$ )

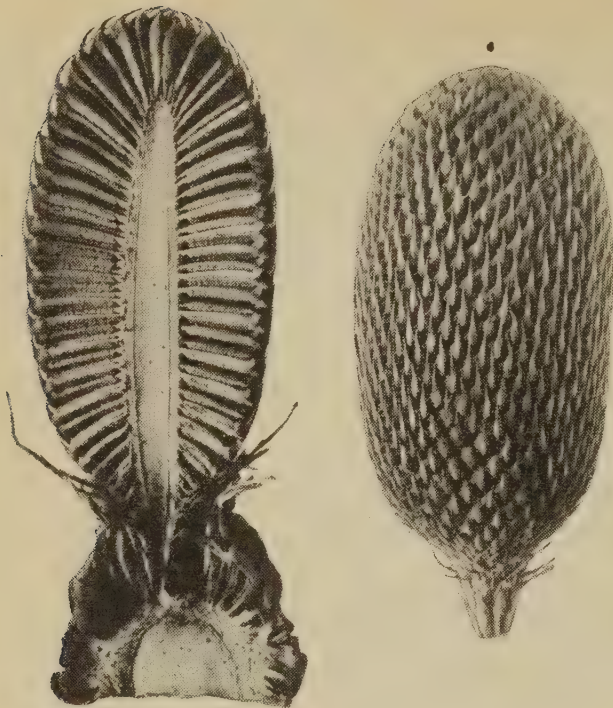


FIG. 460. Cone of microsporophylls of *Cycas*

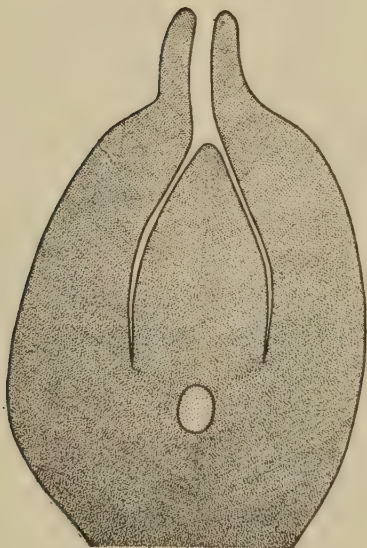


FIG. 461. Longitudinal section through megasporangium of *Cycas rumphii*

The megasporangium consists of the nucellus surrounded by an integument; within the nucellus is a young, rounded, female prothallus. ( $\times 20$ )

the pollen grains are shed. The pollen grains are carried by the wind and enter the megasporangia through the micropyles. Here the pollen grain sends out a pollen tube which grows from the tube cell, becomes embedded in the nucellus, and, by elongating, pushes the prothallial and generative cells through the nucellar region toward the archegonia (Figs. 465, 468). The *generative cell* later gives rise to a sterile stalk cell and a large body cell (Figs. 465, 468). The latter produces two *spermatozooids* (Fig. 468). These are large ciliated structures which have the ability to swim. The pollen tube approaches an archegonium and discharges the spermatozooids, one of which enters the archegonium and fuses with the egg cell (Fig. 466).

The ciliated spermatozooids in a highly developed land plant show the survival of a character acquired by aquatic ancestors.

**Seed.** The fertilized egg develops and produces an embryo which remains embedded in the prothallus



(Figs. 464, 469). After the embryo reaches a certain size the seed is mature. In the mature seed the embryo is surrounded by the prothallus, and the prothallus is surrounded by the integument, the nucellus having largely disappeared (Figs. 464, 469). The prothallus contains a very considerable supply of stored food. During germination the embryo lives on this supply of stored food until it has developed sufficiently to be independent.

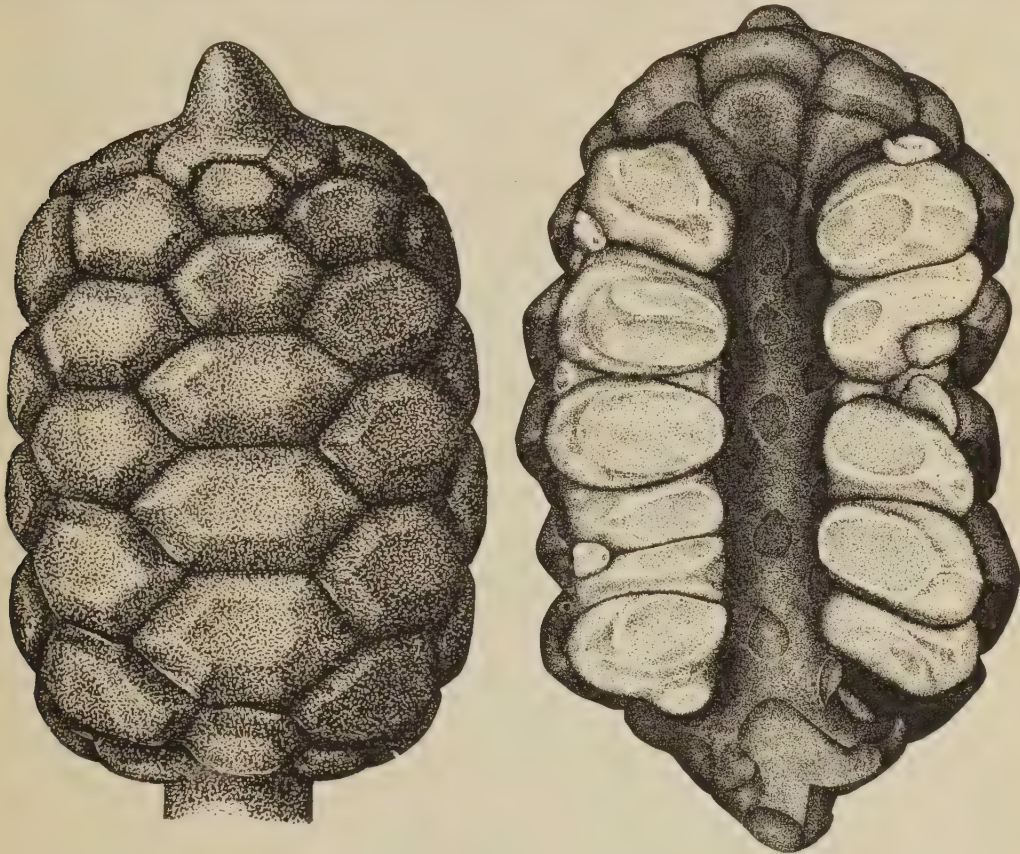


FIG. 462. Cone of megasporophylls of *Zamia floridana*  
Left, entire cone ; right, cone with some sporophylls removed and  
showing seed. ( $\times \frac{2}{3}$ )

**Alternation of generations.** In the cycads there is an alternation of generations, just as in ferns and in liverworts. In the cycads the sporophytic generation produces megaspores and microspores. The spores give rise to the gametophytes. The female gametophyte is a prothallus that is developed within the megasporangium, while the male gametophyte develops from a microspore, or pollen grain. Just as in the ferns, the number of chromosomes is reduced when a spore mother cell divides to form spores. Therefore the spores and

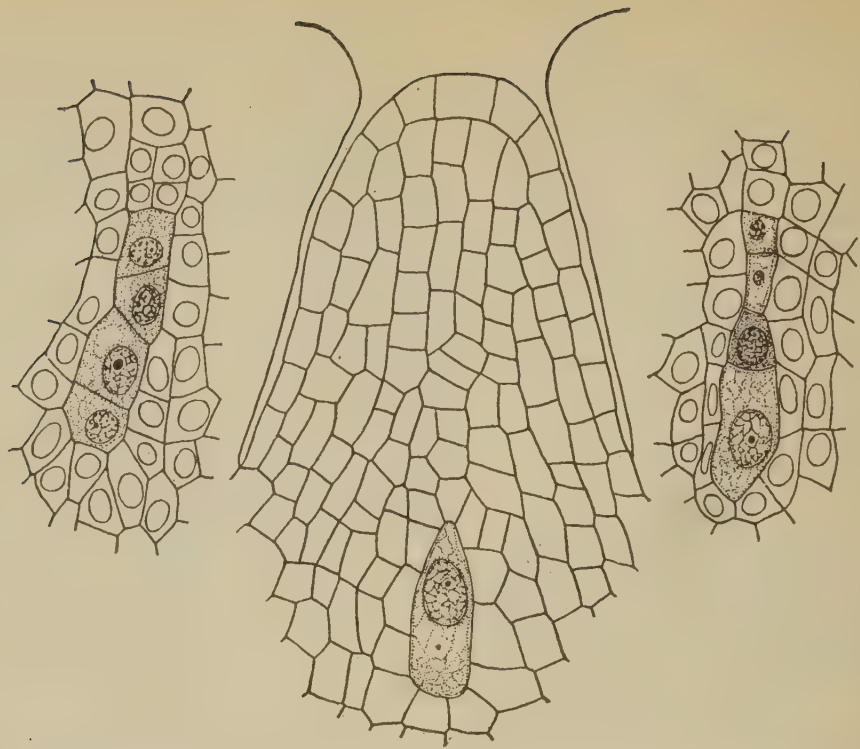


FIG. 463. Megaspore mother cell and megaspores of *Zamia floridana*

Center, megaspore mother cell within the nucellus, the curved lines outside the nucellus showing location of the integument; left, four megaspores formed by the division of megaspore mother cell; right, the three apical megaspores have begun to disorganize, while the lowest, which will give rise to the female prothallus, is enlarging. (Redrawn after F. Grace Smith)

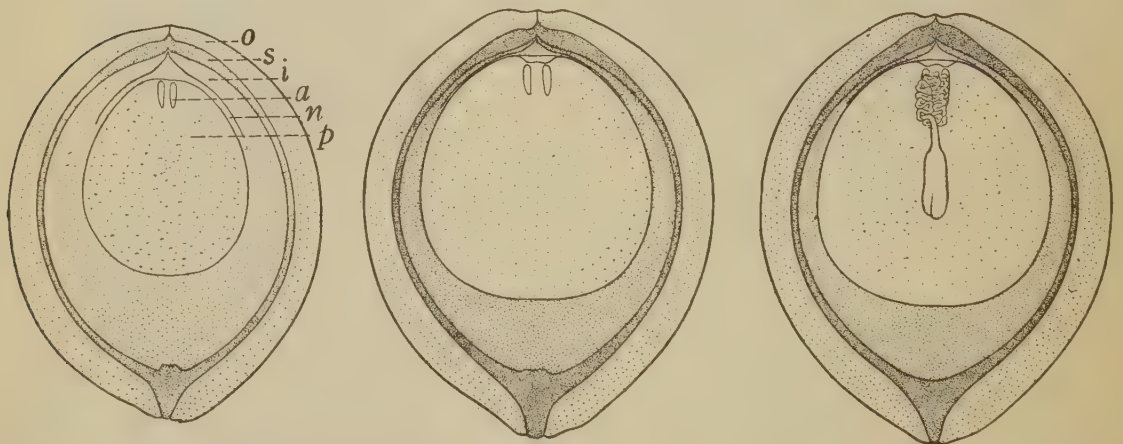


FIG. 464. Longitudinal section through megasporangia of *Cycas rumphii*

Left, megasporangium some months before fertilization; *o*, outer layer of the integument; *s*, stony layer of the integument; *i*, inner fleshy layer of the integument; *n*, nucellus; *p*, female prothallus; *a*, archegonium. Center, an older megasporangium; the prothallus has enlarged while the nucellus has largely disappeared. Right, an embryo has grown from one of the archegonia and penetrated into the prothallus. ( $\times \frac{10}{13}$ )



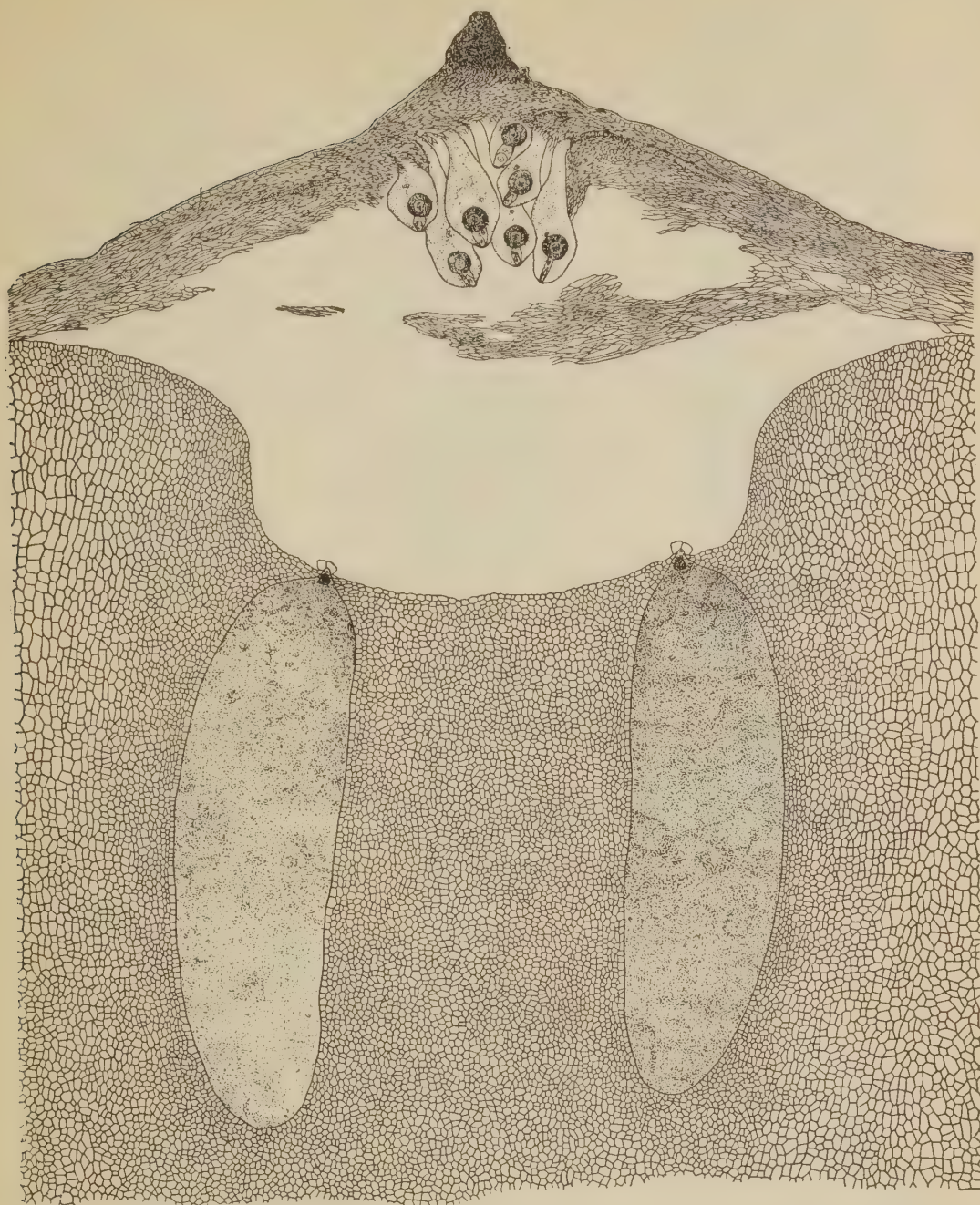


FIG. 465. Longitudinal section of apical portion of megasporangium of *Cycas rumphii* shortly before the time of fertilization

Above is the nucellus, through which pollen tubes are growing; below is a portion of the female prothallus, showing two archegonia

the gametophytes produced by them have the  $x$ , or single, number of chromosomes, while the  $2x$ , or double, number of chromosomes is restored when a sperm nucleus fuses with the egg nucleus. This double number persists throughout the life of the sporophyte and is reduced again when a spore mother cell divides to form four spores.



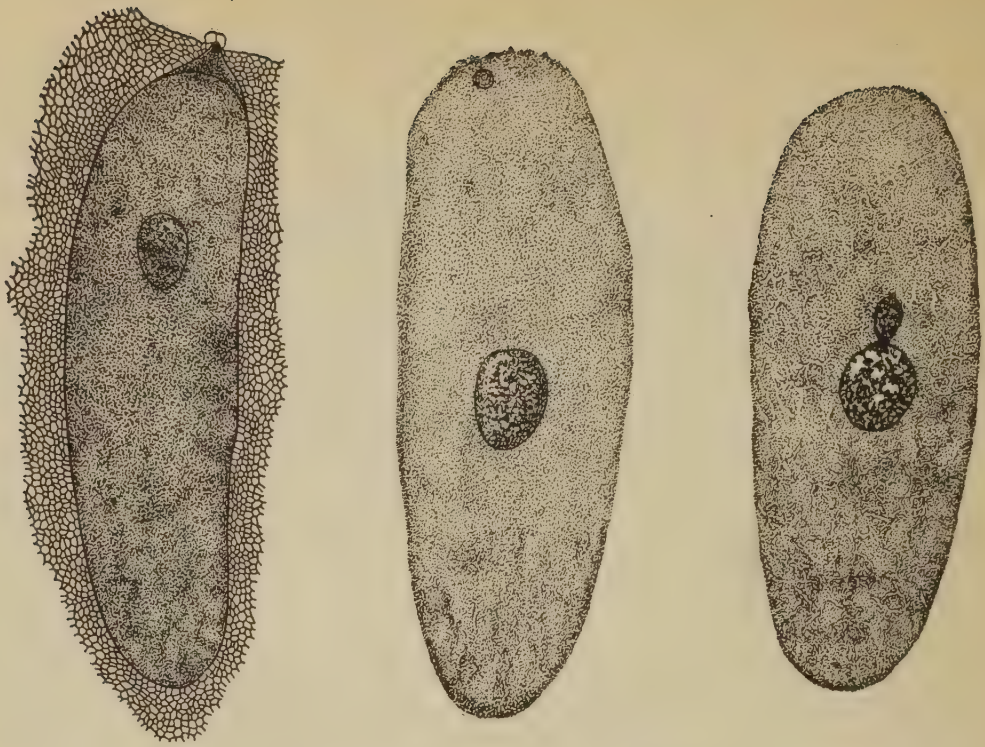


FIG. 466. Archegonia and eggs of *Cycas rumphii*

Left, archegonium in the upper part of which the ventral-canal nucleus and surrounding cytoplasm are disintegrating ( $\times 17$ ) ; center, an egg into the upper portion of which a spermatozoid has penetrated ( $\times 22$ ) ; right, an egg with the nucleus of the spermatozoid about to fuse with the egg nucleus ( $\times 22$ )

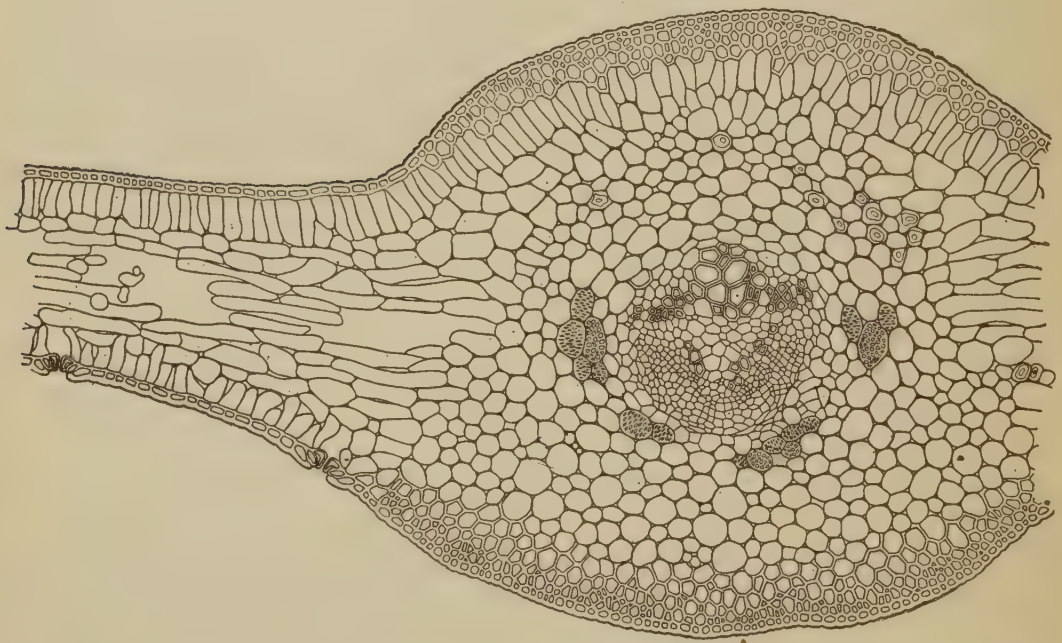


FIG. 467. Cross section of a portion of a leaf of *Cycas*, showing midrib and portion of thin part of blade. ( $\times 50$ )



In the cycads the prothallus, or female gametophyte, is retained permanently within the sporophyte, and even the young sporophyte begins its development under the protection of the previous sporophytic generation. Thus the gametophyte, which



FIG. 468. Pollen grains and pollen tubes of *Cycas*

Upper left, pollen grain of *C. rumphii* before division of nucleus ( $\times 1080$ ). Lower left, pollen grain of *C. rumphii* after the formation of male prothallus ( $\times 1080$ ); above is the large tube cell, below this the generative cell, below the generative cell the prothallial cell. Center, pollen tube of *C. rumphii* before division of cell ( $\times 87$ ): *t*, tube nucleus; *b*, body cell; *s*, stalk cell; *p*, prothallial cell. Right, pollen tube of *C. circinalis* with two spermatozoids. (Last figure redrawn after Miyake)

in the liverworts is the dominant phase and in the ferns an independent plant, is reduced in the cycads to a condition in which it is parasitic on the sporophyte. On the other hand, the sporophyte is much more highly specialized in the cycads than in any of the pteridophytes.

**Relationship.** The cycads are descended from an extinct order of plants, the *Cycadofilicales*, which in turn were derived from

ferns or fernlike ancestors. In general appearance the *Cycadofilicales* were so fernlike that their leaves were believed to be the fronds of ferns, until seeds resembling those of the cycads

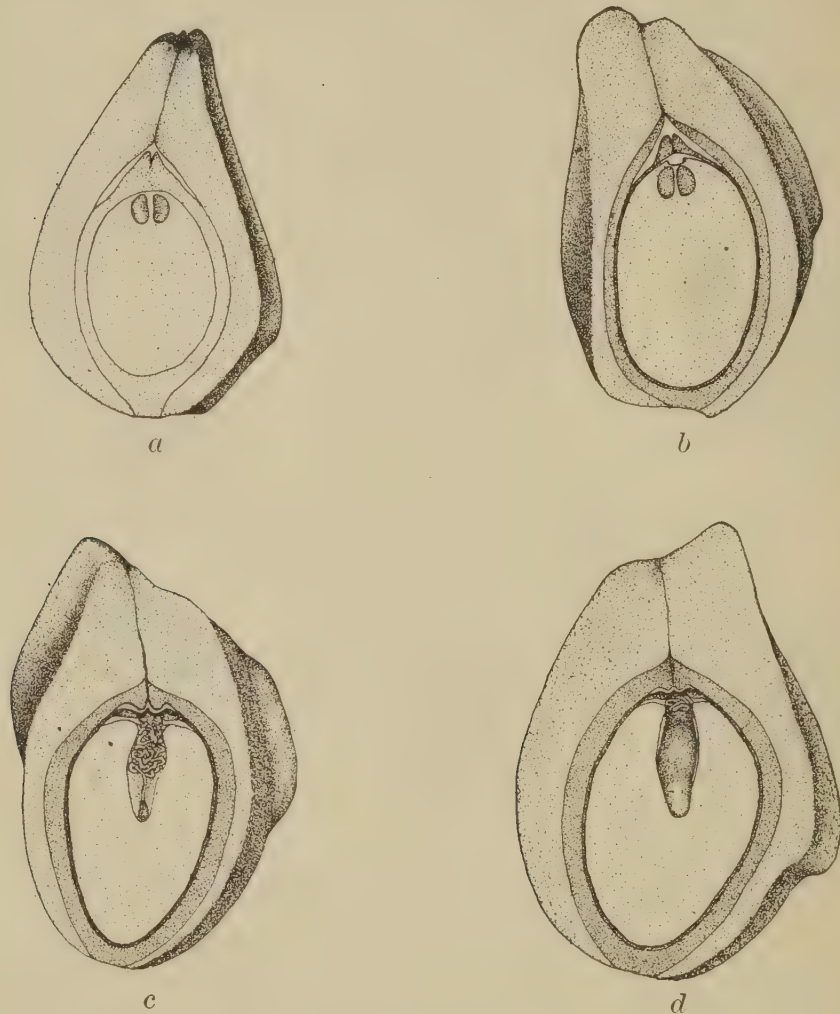


FIG. 469. Longitudinal section of seed of *Zamia*

*a*, female prothallus with two archegonia inclosed in a nucellus, and this within the integument; *b*, older stage in which the nucellus has largely disappeared; *c*, early stage in the development of the embryo (note the long coiled structure, suspensor, which pushes the embryo into the prothallus); *d*, mature seed consisting of embryo surrounded by prothallus and this by the seed coat formed from the integument. The seed coat consists of three layers, a thin fleshy inner layer, a thick stony layer, and a still thicker fleshy outer layer. ( $\times 1\frac{1}{2}$ )

were found attached to them. The vascular anatomy was fernlike but with very well-marked secondary thickening in the stem.

Modern cycads still show fernlike characters. The leaves resemble those of ferns and in some cases are rolled up when



young, like those of ferns. In certain species fernlike vascular bundles are found in the leaves. Even the megasporophyll of *Cycas revoluta* bears some resemblance to the frond of a fern.

In former geologic ages the cycads were much more numerous and important than at present, but they have been crowded out by the development of higher types, and today we see only a remnant of what was once an important group.

#### ORDER GINKGOALES

This order is represented by a single living species of *Ginkgo*, native of China and Japan, but now widely cultivated in temperate countries.

*Ginkgo* is of interest as showing characters intermediate between those of the cycads and the conifers.

*Ginkgo* is of interest as showing characters intermediate between those of the cycads and the conifers. It resembles the conifers in general habit, as it is a tall, branching tree. The stem, like that of the conifers, has a small pith and a wide, woody cylinder. In the size of its fan-shaped leaves *Ginkgo* also approaches the conifers. The megasporangium is very much like that of the cycads (Figs. 470-472), and fertilization is by means of motile spermatozoids formed in pollen tubes. Among living seed plants motile spermatozoids are found only in the two most primitive existing orders of gymnosperms, the *Cycadales* and *Ginkgoales*. When *Ginkgo* is compared with the cycads and the conifers, it is found to be closer to the latter in general vegetative structure and to resemble the former in the character of the megasporangium and the method of fertilization.

**Relationship.** *Ginkgo*, while having characters which make it intermediate between the cycads and the conifers, does not appear to have been derived from cycads or to be ancestral to



FIG. 470. *Ginkgo biloba*

End of branch bearing young leaves and young megasporangia. ( $\times \frac{1}{2}$ )

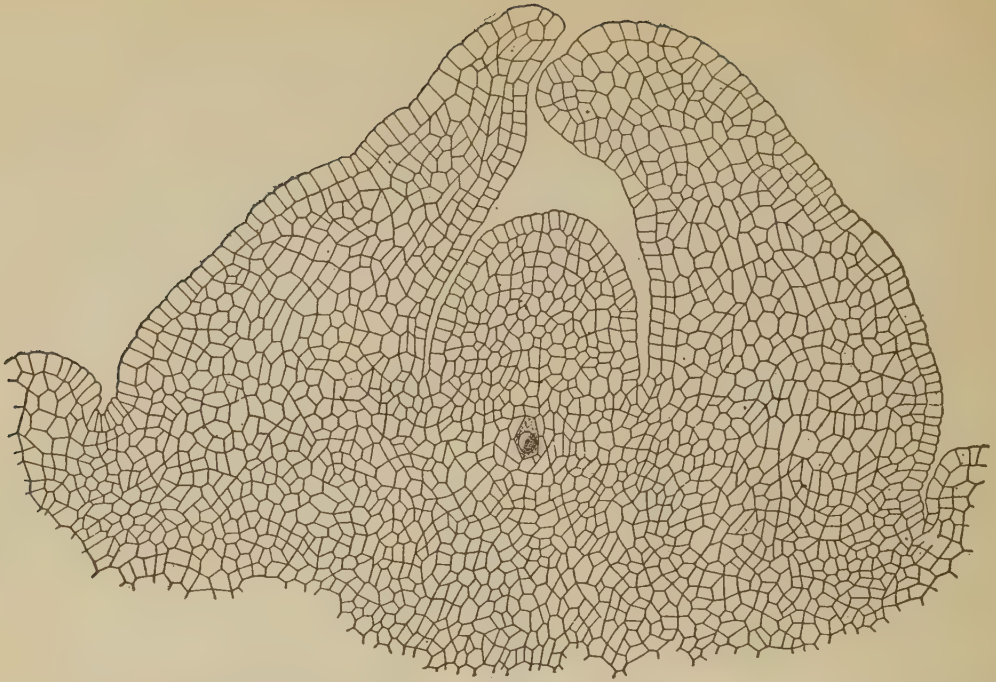


FIG. 471. A longitudinal section through megasporangium of *Ginkgo*, showing nucellus containing megaspore mother cell and surrounded by integument. ( $\times 85$ )



FIG. 472. Branch of *Ginkgo* with seeds which have developed from megasporangia. ( $\times \frac{1}{2}$ )



conifers. It is generally believed that both it and the conifers are descended from an extinct order of gymnosperms, the *Cordaitales*, which was a dominant element of the flora of the

Paleozoic Age. This relationship explains the similarities between *Ginkgo* and the conifers. The *Cordaitales* appear to have been derived either from the *Cycadofilicales* or



FIG. 473. Branch of *Ginkgo* bearing strobili of male sporophylls. ( $\times \frac{2}{3}$ )

from their ancestors, so that *Ginkgo* is related through the *Cycadofilicales* to the *Cycadales*. While the cycads and *Ginkgo* have some primitive features in common, the cycads have retained primitive characters to a greater extent than has *Ginkgo*. A diagrammatic representation of the relationship of *Ginkgo* is clearly shown in Fig. 474.

*Ginkgo* is almost unknown in the wild state, and the order *Ginkgoales* was on the road to extinction when *Ginkgo* began to be cultivated. In former ages the order included a number of genera and had a wide distribution.

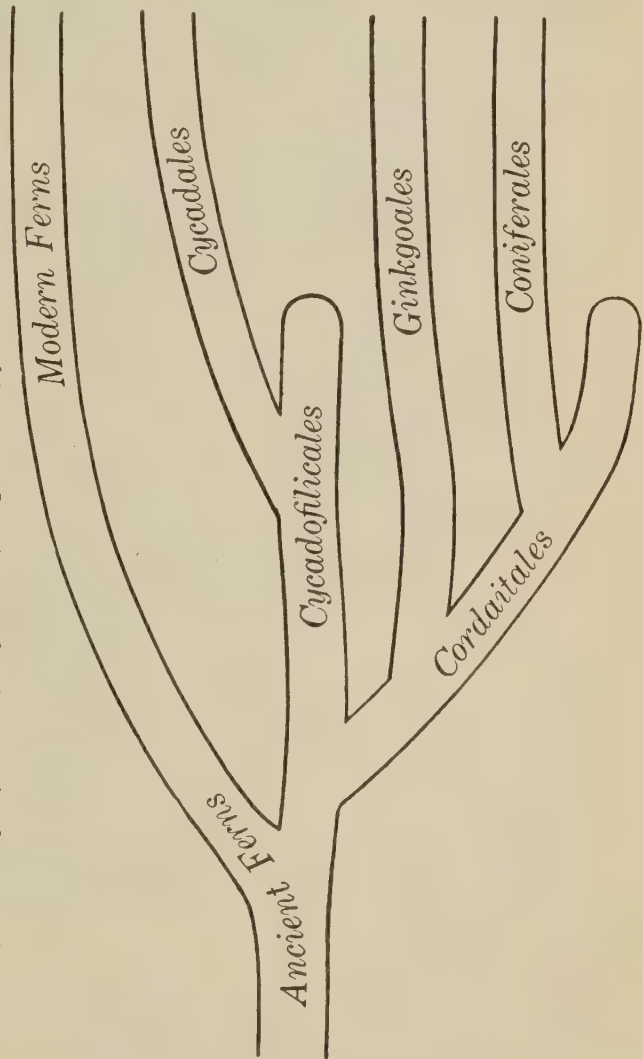


FIG. 474. Diagram showing relationship of gymnosperms

ORDER *CONIFERALES*

The conifers are woody plants ranging in size from shrubs to the giant *Sequoia* of California. Many of them contain numerous resin canals (Fig. 121).

**Leaves.** The leaves are xerophytic (Fig. 475), are usually small, and in many species are needlelike or scalelike. In a few

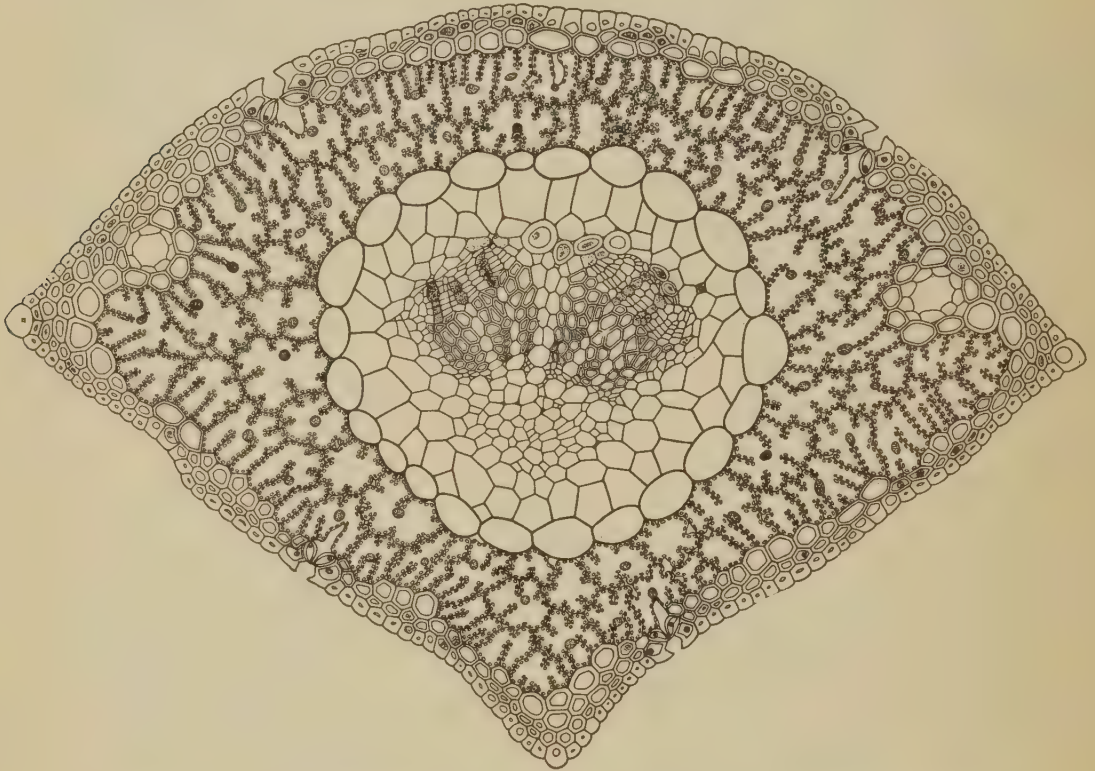


FIG. 475. Cross section of leaf of pine (*Pinus insularis*)

genera the lamina is rather broad (Fig. 476). The leaves usually remain on the plant for several years, being deciduous in only three genera.

**Stem structure.** The arrangement of the vascular bundles and of the secondary thickening of the conifers is very similar to that of dicotyledonous angiosperms. There is a small pith surrounded by a wide woody cylinder. The structure of the wood differs from that of dicotyledons in that it contains only tracheids and wood parenchyma and lacks vessels and wood fibers (Fig. 130). The tracheids serve both for water conduction and as strengthening elements. Owing to the absence of vessels and



wood fibers the wood of the conifers is much more primitive than that of the flowering plants. The xerophytic structure of the leaves is connected with the primitive nature of the wood and the large size of the plants, as tracheids are not as well fitted for conducting large quantities of water as are vessels.

**Sporangia.** The *microsporangia* are small and are borne in small cones. In the majority of genera the *megasporangia* are also in distinct cones, and the seed when ripe is dry. In some genera the cone is so greatly reduced as not to have the appearance of a cone and produces only a single ovule, and in this case the seed is more or less surrounded by a fleshy covering.

**Pine.** The pine (Fig. 478) is such

a widely distributed, well-known, and typical conifer that it may be taken as a good example of the order known as *Coniferales*.

**Vegetative structure.** The crown has a conical form, owing to the fact that both the central stem and the branches have an



FIG. 476. *Agathis alba*, the source of Manila copal  
Lower left, female cone; lower right, small branch  
with male cones ( $\times \frac{1}{3}$ )



excurrent form of growth. The branches are of two kinds, long branches and short branches with limited growth. The only leaves on the long branches are scale leaves (Fig. 479), a feature not characteristic of all conifers. The short branches arise in the axils of

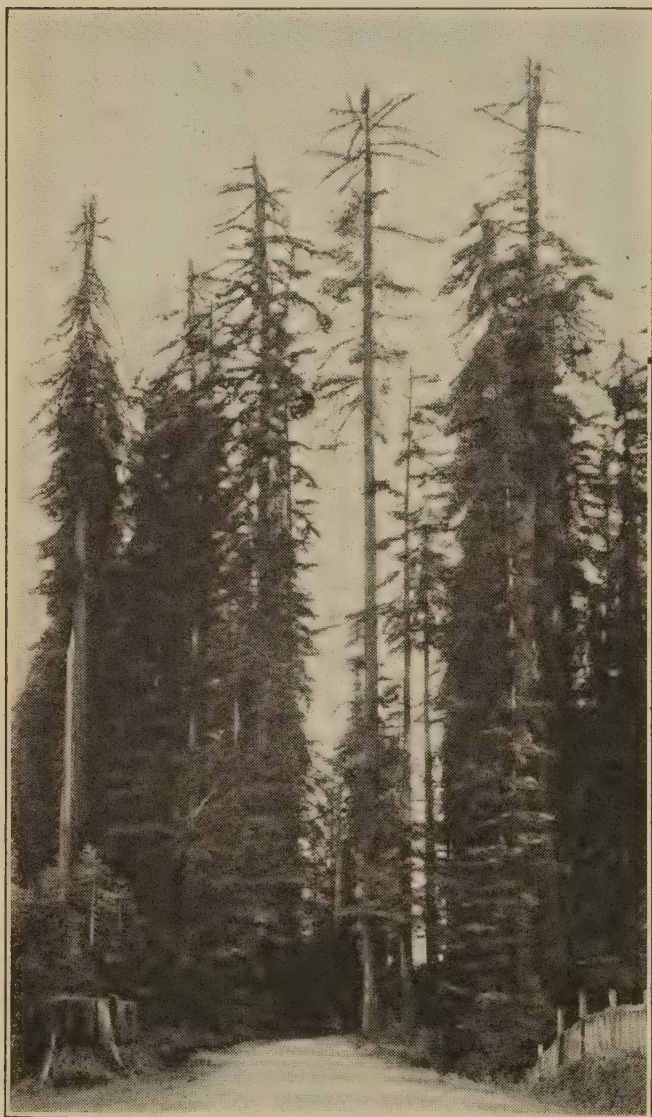


FIG. 477. Three-hundred-foot redwood, Humboldt County, California

the scale leaves and bear needle-shaped green leaves, singly or in clusters (Fig. 479). The short branches are deciduous, being shed with the leaves (Fig. 479).

**Megasporangium and female prothallus.** The megasporangia (ovules) are produced in cones (Fig. 479). The cones terminate special short branches. Each sporangia-bearing component of the cone consists of a bract and above this an ovuliferous scale with two megasporangia (Fig. 479). This compound structure does not seem to be a simple megasporophyll, but there is great difference of opinion as to its morphological nature. The ovuliferous scales are the conspicuous scales in

the mature cone. The megasporangia occur near the base of the ovuliferous scale and are directed toward the central axis of the cone.

The megasporangium resembles that of the cycads in that it consists of a nucellus surrounded by a single integument (Fig. 451). A megaspore mother cell is formed within the nucellus and divides to form a row of four megaspores (Figs. 451, 452).



The three apical megaspores degenerate, while the basal one germinates (Fig. 452) and produces a female prothallus (Fig. 453) which, as in all of the spermatophytes, remains permanently inclosed within the megasporangium. The female prothallus is a white, oval mass, at the apical end of which archegonia are produced. A mature archegonium consists of a large egg cell and the neck cells (Fig. 480). At one stage there is an evanescent ventral-canal cell. A comparison of the cycads and the pine shows that the general structure of the ovules and female prothalli is very similar in the two cases.

**Microsporangium.** The microsporophylls are small and borne in small cones (Fig. 481). Each has two microsporangia on its under surface. The male cones

occur in clusters near the ends of the long branches and, like the short branches, are produced in the axils of the scale leaves on the long branches (Fig. 481).

**Pollination.** The microspores (pollen grains) are carried by the wind and deposited in the micropyles of the megasporangia. This process is known as pollination. At the time of pollination the female cone stands erect and the scales are spread apart

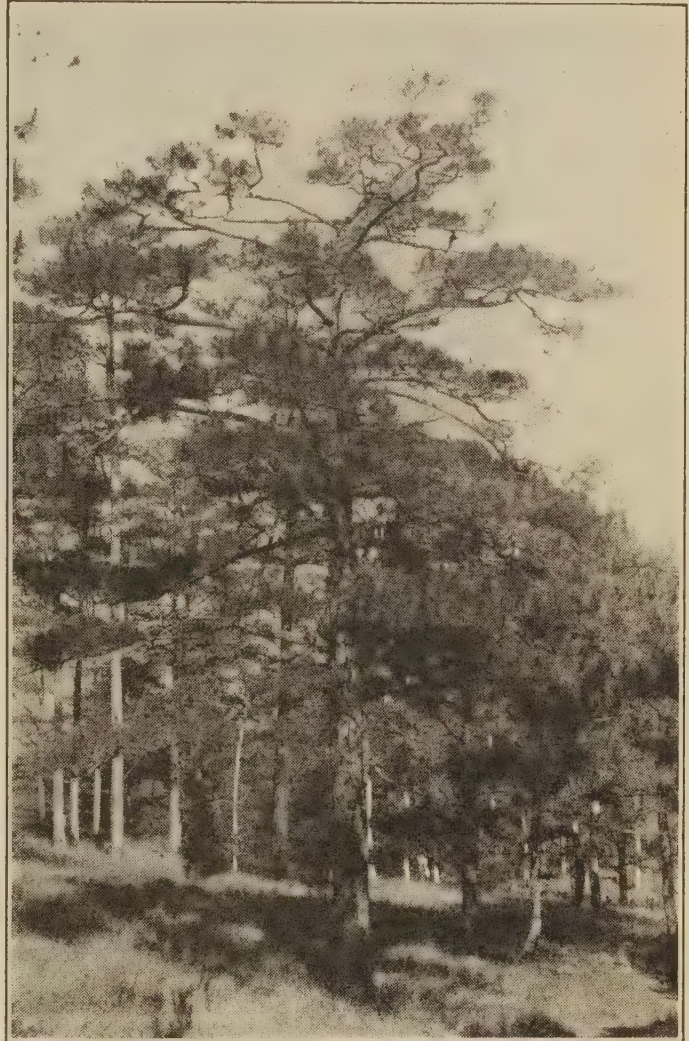
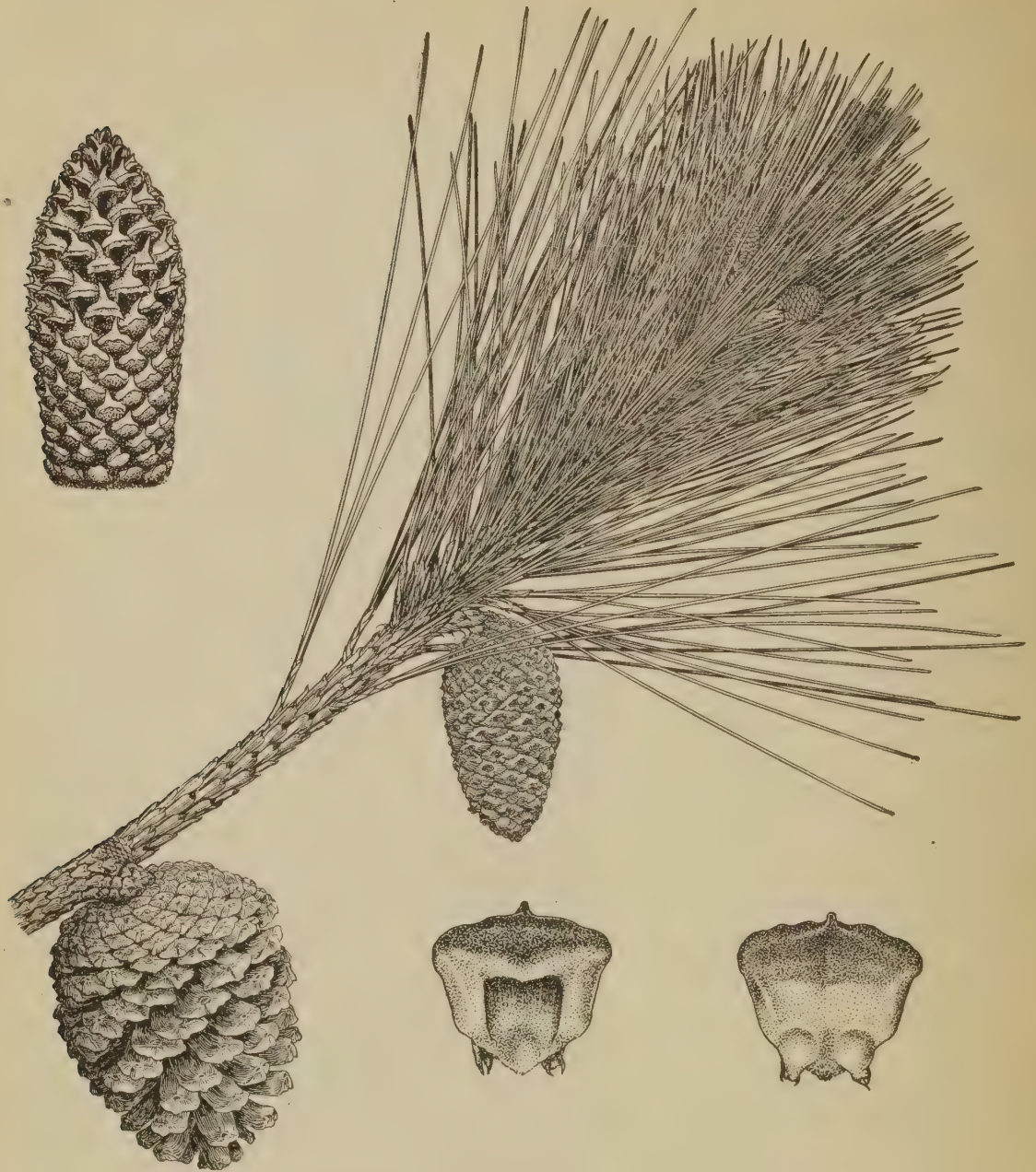


FIG. 478. *Pinus insularis* forming an open forest in the mountain region of Luzon, in the Philippine Islands



FIG. 479. Pine (*Pinus insularis*)

Center, a branch bearing cones of three different years. The small ones at the tip have recently been pollinated, the next in age is about a year old, while the oldest has opened to shed its seeds ( $\times \frac{1}{3}$ ). Upper left, a cone at the age of pollination. Note that the sporophylls are separated so that the pollen can enter between them ( $\times 3\frac{1}{2}$ ). Lower right, young scale, first as seen from below, showing bract, and then as seen from above, showing two ovules ( $\times 6$ )

(Fig. 479), so that microspores can reach the megasporangia. After pollination the short stem bearing the female cone bends downward so that the cone hangs vertically, and in this position it remains during the remainder of its existence (Fig. 479).



**Male gametophyte and fertilization.** The microspore (Fig. 482), before being shed, germinates, and a male gametophyte, or prothallus, is formed within the spore wall (Fig. 482). This consists of four cells: a *tube* cell, a *generative* cell, and two evanescent *prothallial* cells which begin to disorganize as soon as they are formed, so that only remnants of them appear in the pollen grain at the time of shedding. After reaching the micropyle the pollen grain sends out a pollen tube (Fig. 483) which grows through the nucellus and enters the archegonium. During the growth of the pollen tube the tube nucleus migrates into the tube, and the generative cell divides to form two cells: a *stalk* cell (toward the degenerating prothallial cells) and a *body* cell (Fig. 483). Later the body cell becomes free and passes into the tube, where its nucleus divides to form two male nuclei. Fertilization results from the fusion of one of the male nuclei with an egg nucleus.

The most striking difference between the sexual method of reproduction in the conifers and that in the cycads and *Ginkgo* is that in the conifers there are no ciliated spermatozoids. The presence of ciliated spermatozoids is a character, derived from aquatic ancestors, which has persisted throughout the division *Pteridophyta* and among the *Gymnospermae* in the *Cycadales* and *Ginkgo*, but has disappeared in the *Coniferales* and all the higher orders of the *Spermatophyta*.

**Seed.** The fertilized egg germinates and produces an embryo which remains embedded in the prothallus until the germination

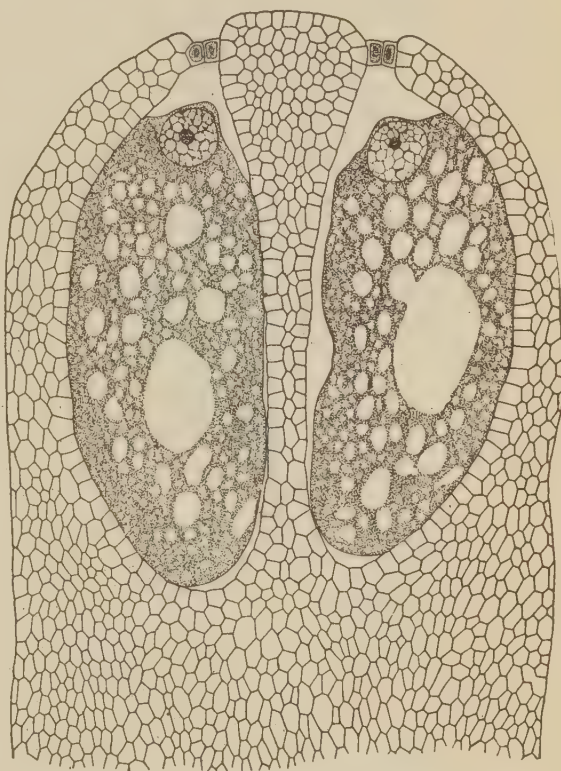


FIG. 480. Apex of female prothallus of pine, showing two archegonia.  
( $\times 75$ )



FIG. 481. Left, branch of *Pinus insularis* bearing male cones ( $\times 1$ ); right, longitudinal section through a male cone ( $\times 5$ )

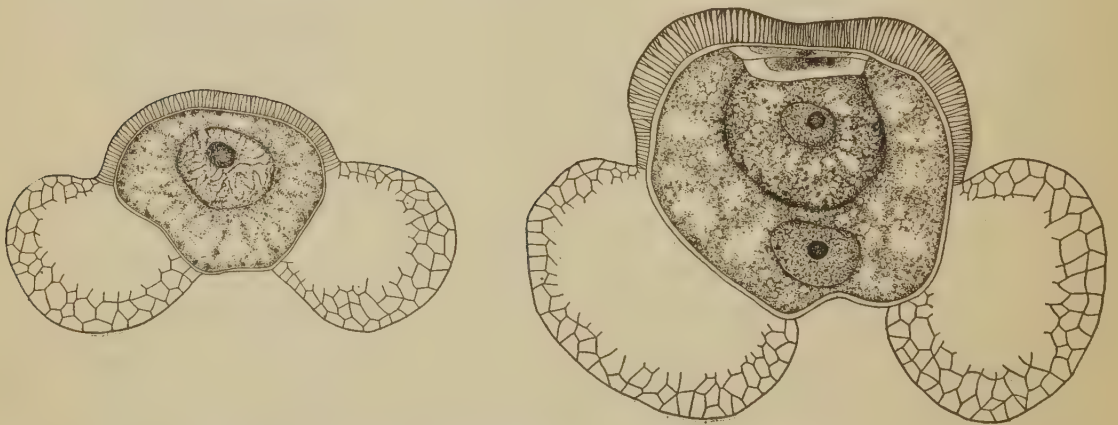


FIG. 482. Male gametophyte of pine

Left, section of microspore of pine; note the inflated wings which make the spore buoyant ( $\times 390$ ). Right, male prothallus within the wall of the microspore of pine: above are two disorganizing prothallial cells; below these is the generative cell; and below and almost surrounding this is the large tube cell ( $\times 530$ )



of the seed. The embryo is a cylindrical structure with a number of cotyledons. The integument forms the seed coat (Fig. 454).

**Alternation of generations.** In the conifers the alternation of generations is very similar to that described for the cycads. The sporophyte is a large plant which produces megaspores and microspores. The megaspore gives rise to a female gametophyte, or prothallus, bearing archegonia, while the microspore produces a male gametophyte. The fertilization of the egg in the archegonium results in the production of a sporophyte. There is, thus, as in the *Bryophyta* and the *Pteridophyta*, an alternation of a sporophytic and a gametophytic generation. As in bryophytes, pteridophytes, and cycads, the sporophyte is characterized by a double number of chromosomes, reduction taking place during the division of the spore mother cells. The gametophyte has the single number of chromosomes, the double number being restored at fertilization.

**Relationship.** The *Coniferales* appear to be descended from an extinct order of gymnosperms, the *Cordaitales*, which either were derived from or were closely related to the *Cycadofilicales*. As the *Cycadofilicales* gave rise to the *Cycadales*, the *Coniferales* are related through the *Cycadofilicales* to the *Cycadales*. The cycads, as we have seen, are much more primitive than the conifers. A diagrammatic representation of the relationships of these orders is clearly shown in Fig. 474.

**Distribution.** There is a striking difference in the distribution of cycads and of conifers. The former are tropical and subtropical, while the latter are found largely in temperate zones. They



FIG. 483. Pollen tube of pine

Below, near the apex, is the tube nucleus. Above, and still within the spore wall, is the stalk cell next to the spore wall and, adjoining this, the body cell. (Redrawn after Miss Ferguson)

are particularly characteristic of north-temperate regions, where they form valuable forests of great extent. Conifers are frequently numerous on tropical mountains, and in limited areas may be the dominant element of the flora.

### CLASS ANGIOSPERMAE

The angiosperms are the culmination of the evolutionary process in plants. In them the sporophyte has reached its greatest

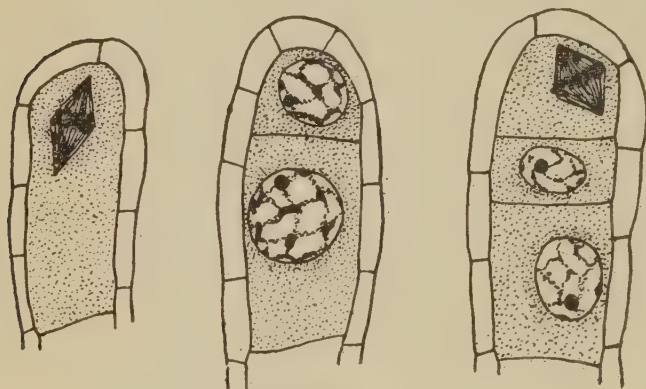


FIG. 484. Megaspore mother cell and megaspores of an orchid

Left, megaspore within nucellus; center, megaspore is divided into two daughter cells; right, lower daughter cell has divided into two megaspores, while the upper one is in process of division. (Redrawn after Brown and Sharp)

specialization, while the gametophyte has become greatly reduced. They are the dominant element of our land flora, and in number of species exceed all other green plants. They include all the woody plants other than the gymnosperms and the tree ferns, and all herbaceous plants other than the ferns and

fern allies. Many of the angiosperms have become specialized for aquatic conditions, and such species form the dominant vegetation of fresh waters. Angiosperms have also invaded salt water, and even here grasslike forms may be the dominant element of the vegetation in rather quiet water where the bottom is muddy.

The angiosperms are divided into two subclasses, the *Dicotyledoneae* (dicotyledons) and *Monocotyledoneae* (monocotyledons). The distinctive characters of these groups have been given in earlier chapters. The most primitive dicotyledons appear to have been woody; it is believed that the herbaceous dicotyledons and the monocotyledons have been derived from woody dicotyledons.



**Sporophyte.** The sporophyte is a complicated plant with roots, one or more stems, leaves, and strobili (aggregations of sporophylls) known as flowers.

The wood is highly specialized in that rows of tracheids have become transformed into vessels, while other tracheids are specialized as wood fibers. The vessels are greatly superior to tracheids for the conduction of water, and in most angiosperms the function



FIG. 485. Development of female prothallus in an orchid

First figure, apical megaspores are disorganizing, while basal megaspore has enlarged and its nucleus has divided to form two nuclei. Second figure, older stage, showing formation of vacuole. Third figure, nucleus at each end has divided, resulting in four nuclei in the prothallus. Fourth figure, telophase of division of four nuclei to form eight. Fifth figure, six nuclei cut off by walls; in the base there are three antipodal cells; at the tip are a large egg cell and two smaller synergids; between the groups of cells are two free polar nuclei. Sixth figure, fusion of the polar nuclei. (Redrawn after Brown and Sharp)

of the tracheids is largely that of mechanical support. The development of an efficient water-conducting system composed of vessels has enabled angiosperms to produce a great display of mesophytic foliage. The improvement in the conducting system has therefore resulted in a great development of the assimilating system.

Another great advance shown by angiosperms is the development of complicated structures which facilitate insect pollination.

**Sporophylls.** There are two kinds of sporophylls, *megasporophylls* and *microsporophylls*. When there is only one megasporophyll the edges are joined to form an *ovary* with a single cavity,

while the tip of the sporophyll is modified as a stigma for the reception of the microspores. Frequently two or more megasporophylls are united to form a compound ovary which may have either one or more cavities (Fig. 205). In this case the tips may form separate stigmas or only a single stigma. The megasporangia (ovules) are inclosed in the ovary by the megasporophylls.



FIG. 486. Formation of male gametophytes in *Elodea*

Left, a tetrad of microspores of an angiosperm (*Elodea*) ( $\times 550$ ); upper right, microspore nucleus has divided, resulting in the formation of a large tube cell and a small generative cell, which in the figure is situated in the lower left portion of the tube cell; lower right, the generative cell has divided to form two male cells ( $\times 205$ )

These microsporophylls of the angiosperms are also known as stamens (Fig. 206), while the microsporangia are the pollen sacs.

These megasporophylls and microsporophylls are borne in flowers, and in complete flowers are surrounded by two sets of modified leaves, the petals and the sepals. The torus is a short stem, and as it bears sporophylls the flower is a modified strobilus.

**Megasporangium and female gametophyte.** In the angiosperms the megasporangium consists of an oval structure, the *nucellus*, or sporangium proper, surrounded by one or two *integuments*. At the apex there is a small opening, the *micropyle*, which extends through the integuments (Fig. 227).

In the nucellus there is usually found a single *megaspore mother cell* (Fig. 484), which in the majority of cases divides to form a row of four *megaspores* (Fig. 484). The three megaspores situated toward the apex of the nucellus degenerate (Fig. 485). The basal megaspore is also known as the *embryo sac*, and within it the female gametophyte, or prothallus, is formed. First the embryo sac increases considerably in size and



becomes oval in outline (Fig. 485). Its nucleus divides and the two daughter nuclei migrate to the opposite ends of the sac. By two successive divisions each of these daughter nuclei gives rise to a group of four nuclei, the groups being at opposite ends of the sac (Fig. 485). At each end three of the nuclei become surrounded by cell walls. The three cells thus formed at the end of the sac away from the micropyle are known as *antipodal* cells. The group of three cells at the micropylar end consists of two cells (*synergids*) and an *egg* cell. The two nuclei which are free in the cytoplasm are *polar* nuclei, and they move to the center of the sac. In this condition the female gametophyte is mature and the egg is ready for fertilization.

In a considerable number of species the megaspore mother cell, instead of forming a row of separate megaspores, becomes the embryo sac.

#### Male gametophyte and fertilization.

The microspore (pollen grain) begins to germinate before it is shed, and forms a male gametophyte, or prothallus, within the microspore (Fig. 486). This gametophyte is produced by the division of the nucleus

of the microspore to form a *tube* nucleus and a *generative* nucleus. The growth of the pollen tube appears to be connected with the activity of the tube nucleus. The generative nucleus divides to form two *male* nuclei. This division usually takes place in the pollen tube, but may occur while the pollen is in the microsporangium (Fig. 486). After being deposited on the stigma the pollen grain sends out a pollen tube into which the nuclei

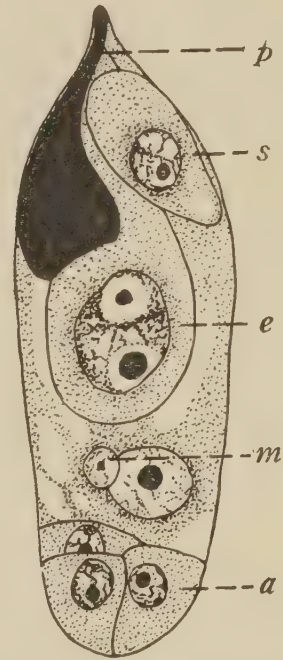


FIG. 487. Fertilization stage in the embryo sac of an orchid

*p*, pollen tube; *s*, synergid; *e*, egg containing nucleus formed by the fusion of male and female nuclei; *m*, male nucleus in contact with nucleus formed by the fusion of two polar nuclei; *a*, antipodal cells. (Redrawn after Brown and Sharp)

migrate. The pollen tube grows down through the style and enters the female prothallus, usually by way of the micropyle (Fig. 4). The two male nuclei are discharged in the embryo sac. One of them fertilizes the egg by fusing with its nucleus (Fig. 487). The fertilized egg germinates and produces an embryo. The second male nucleus and the two polar nuclei fuse to form an *endosperm* nucleus (Fig. 487).

**Endosperm.** The endosperm nucleus undergoes a series of rapid divisions which result in the formation of endosperm tissue around the developing embryo, filling the embryo sac. The nuclei of the cells of this tissue contain a triple, or  $3x$ , number of chromosomes, because the primary endosperm nucleus was formed by the fusion of three nuclei. The endosperm furnishes nourishment for the developing embryo. Usually it completely absorbs the nucellus before the seed is mature. Frequently the embryo absorbs all of the endosperm during the development of the seed; in such cases there is no endosperm in the ripe seed (Fig. 268). In many cases the endosperm persists in the mature seed and is absorbed only during germination (Fig. 269).

**Seed.** When the endosperm is absorbed during the development of the seed, the ripe seed consists of an embryo surrounded by one or two integuments which form the seed coats. If the endosperm persists in the seed, the embryo is surrounded by the endosperm, and this by the seed coats.



## CHAPTER XIV

### PLANT GEOGRAPHY

The physical characteristics of the vegetation of a given region are largely due to environmental conditions, while the systematic relationships depend to a great extent on the past or present geological connections or barriers. When two regions have been separated for a considerable length of time by barriers such as high mountain chains or wide seas, which it is impossible for most plants to cross, the systematic composition of the vegetation in the two regions will be very different. If the environmental conditions are similar, however, the vegetation of two areas, whether separated or not, is likely to have the same general appearance because in most cases similar external conditions produce associations of plants whose fundamental physical characteristics are much alike. In the present chapter the vegetation of the world will be considered from the standpoint of the physical types of vegetation found in various environments. The most favorable environmental conditions for plant growth are found in those lowland regions of the tropics where moisture is abundant and where there is no pronounced dry season. If from moist tropical lowlands we proceed either to colder latitudes, to higher altitudes, or to drier regions, the environmental conditions become less favorable and the vegetation is less luxuriant. Forests of moist tropical lowlands therefore afford a convenient starting point for a discussion of the vegetation of the world.

**Tropical rain forests.** Tropical lowlands, where soil conditions are favorable and where there is no distinct dry season, or where the dry season is not long and severe, produce very luxuriant forests (Figs. 6, 488). Typically, the forest canopy is composed of three stories characterized by different types of





FIG. 488. Rain forest on lower slope of Mount Maquiling, Philippine Islands  
Note the different heights of the trees. The feathery leaves belong to climbing palms (rattans)



trees. The trees of the top, or dominant, story form a nearly closed canopy which is frequently 60 meters or more in height. The crowns of the second story are beneath those of the dominant story and, like those of the dominant story, frequently form a nearly closed canopy. The trees of the third, or lowest, story are usually small and slender and have small open crowns.



FIG. 489. Climbing palms (rattans) in Philippine rain forest

The presence of these three stories of different trees is not usually evident on casual observation, for the composition of all the stories is very complex and few of the trees present any striking peculiarities. Moreover, smaller trees of a higher story always occur in a lower story as well as between the different stories, while the different species of a story have different heights. Erect palms are frequently numerous in the lower stories but are seldom a prominent part of the vegetation.

Beneath the tree stories there is a ground covering, the composition of which varies in different situations. In rather dry areas, particularly on ridges, it may consist largely of woody



plants, while in moist situations, especially in ravines, herbs are abundant. Among the latter, ferns are frequently prominent.

Large vines are always conspicuous in moist tropical forests. Among these are the climbing palms, bamboos, and aroids. In



FIG. 490. An epiphytic bromeliad (*Billbergia*)

Note that the leaves form urn-shaped cups for collecting water, which is absorbed by absorbing hairs on the leaves. ( $\times \frac{1}{10}$ )

the Malayan region the long, feathery leaves of rattans (climbing palms chiefly of the genus *Calamus*) are particularly striking (Figs. 70, 489). Dicotyledonous vines are conspicuous chiefly as large cables hanging from the crowns of the tall trees.

Epiphytic vegetation is abundant but is confined chiefly to the larger branches of dominant trees, where it frequently forms striking aërial gardens. The conspicuous epiphytes are ferns and flowering plants, orchids (Fig. 2) being very numerous.

In the American tropics, bromeliads (Fig. 490) are conspicuous. The epiphytes have a xerophytic structure, many of them containing abundant water-storing tissue.

The most striking feature of moist tropical forests is the great development of foliage, which is usually continuous from the ground covering to the top of the forests. Although the forest consists chiefly of large trees, what strikes the eye is not the gigantic trunks but rather the foliage which hides the trunks (Fig. 491). In some tropical forests the canopy is exceedingly



dense and there is little development of undergrowth and ground covering. Here the trunks of the trees stand out as gigantic columns. The great luxuriance of tropical rain forests is explained by the fact that moisture, temperature, and light are continuously favorable. The same favorable conditions, particularly in regard to moisture, are responsible for the great development of epiphytes. Large epiphytes are more dependent on a



FIG. 491. View in rain forest on lower slope of Mount Maquiling, Philippine Islands

Note the density of the foliage, which hides the large tree trunks

continuous supply of atmospheric moisture than are terrestrial plants, and they cannot stand prolonged periods of adverse moisture conditions, whether these are due to lack of atmospheric moisture or to cold. In keeping with the great luxuriance of the vegetation, the number of species of trees, vines, and epiphytes in moist tropical forests is greater than in less favored regions. More than a hundred species of trees have been counted on a quarter of a hectare.



Flowers are usually inconspicuous in the forest. This is due to the fact that the production of flowers is extended over a long period instead of being crowded into a short flowering season, and to the fact that as one views the canopy from below the flowers are largely hidden by the foliage.

Tropical forests have been considered as the home of bizarre plants. If the large number of species found in tropical forests



FIG. 492. Base of a tree trunk showing buttress roots

is taken into consideration, the number of curious species in the tropics is probably no greater in proportion to the total number present than in other regions. If by *curious* is meant "specialized," or different from the great majority of plants, then certainly desert vegetation is much more bizarre than is the vegetation of the moist tropics. The vegetation of the temperate zone, with its deciduous leaves, annual rings of growth, highly specialized bud scales, and other features connected with the winter season, is much more specialized than is tropical vegetation. Moist tropical vegetation contains a greater wealth of forms than is found in less favored localities. Among these



forms are many, such as climbing palms (Figs. 70, 489) and begonias, not found elsewhere. Such plants are hardly more peculiar in themselves than are other plants. That such plants have been described as peculiar is largely because they are unfamiliar in the native homes of those who have described them.

A number of interesting types of plants do, however, occur in moist tropical forests (Fig. 74). Strangling figs (Figs. 199, 200)

present a very peculiar appearance and are sometimes numerous. Trees with large buttress roots are rather common (Fig. 492). In a considerable number of species, flowers and fruits occur on the trunks and the large branches, but such species constitute a very small, inconspicuous proportion of all the trees present. Humus-collecting epiphytic ferns (Figs.



FIG. 493. *Drynaria*, an epiphytic fern which has small humus-gathering leaves and large leaves which carry on photosynthesis and produce spores. ( $\times \frac{1}{18}$ )

85, 493) are sometimes abundant. Curious plants of the Malayan region also include large flowering parasites (Figs. 7, 161) and plants that have swollen stems (Figs. 176, 177) which are inhabited by ants, but such plants are usually rare and never form a conspicuous part of the vegetation.

**Subtropical and warm temperate rain forests.** In subtropical and warm temperate regions, where rainfall is abundant and well distributed throughout the year, there are evergreen forests. Near the tropics these are similar to the tropical rain forests, but as colder latitudes are reached the forests partake more of the character of the deciduous forests of the cold temperate regions.

Subtropical and warm temperate forests are generally of lower stature than are the tropical rain forests, and they have fewer woody vines and epiphytes. Subtropical or warm temperate forests occur in southern Japan, Florida, northern Mexico, New Zealand, southeastern Australia, and parts of South America. In southeastern Australia they are found in gullies and valleys,



FIG. 494. Deciduous forest in northeastern part of the United States

and their luxuriance is due more to subterranean water than to rain. The rain forests of Australia and New Zealand are characterized by a great abundance of tree ferns.

**Cold temperate deciduous forests.** In cold temperate regions there are two classes of forests: the deciduous broad-leaved forests (Fig. 494) and the evergreen needle-leaved, or coniferous, forests (Fig. 495). The cold winter season, from a physiological standpoint, is a dry period, owing to the fact that low temperature hinders the absorption

of water by the roots. In broad-leaved forests the lessened ability of the roots to absorb water is counterbalanced by the loss of the leaves, and so the trees are leafless during the winter season (Fig. 496). These deciduous forests are very much less luxuriant than the tropical rain forests. The trees form only a single story, and when this is well developed there is scanty development of undershrubs and herbs. The space under the main canopy is therefore open (Fig. 497), instead of being densely filled as is the case in most of the tropical rain forests.



Climbing vines are scarce and confined chiefly to the edges of the forests. Epiphytes are also scanty and, except in the warmer parts of temperate zones, consist only of bryophytes, lichens, and algæ. The best development of deciduous forests occurs in the eastern portion of the United States.

During the winter season the buds of most of the species are protected by specialized scales which prevent the buds from being desiccated (Fig. 94). The time of growth and development of the leaves is determined by the seasons. The winter buds contain the flowers and leaves of the coming spring and summer. The flowers usually expand at the beginning of the growing season, before the leaves appear or are fully developed. The leaf buds open and the leaves expand very rapidly. The foliage is fully developed early in the season, and the expansion of new leaves then ceases. During the latter

part of the season the buds that will expand during the next spring are formed, and food material, which will make possible rapid growth in the spring, is stored in the stems.

The expansion of the foliage early in the season is of great advantage, as it allows all the leaves to function for the greatest possible length of time. The early appearance of flowers

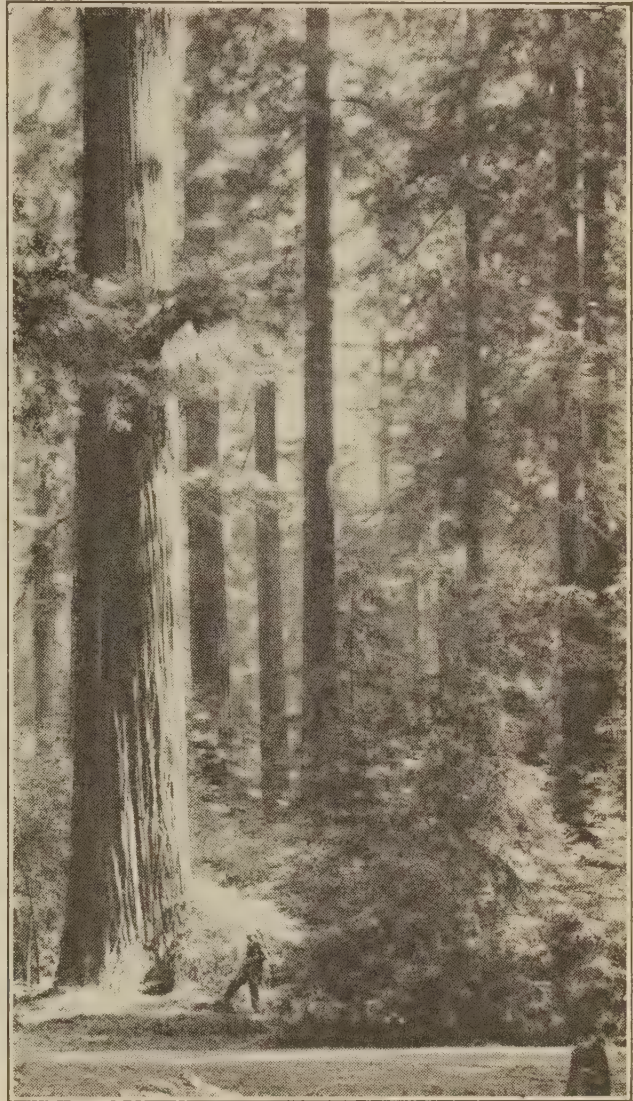


FIG. 495. Redwood forest, Humboldt County, California



allows time for the development of the fruit and at the same time facilitates pollination, as both wind and insects have freer access to the flowers in a leafless forest than in one in full foliage.

One of the most striking characteristics of the forests is the behavior of small perennial herbs with persistent underground

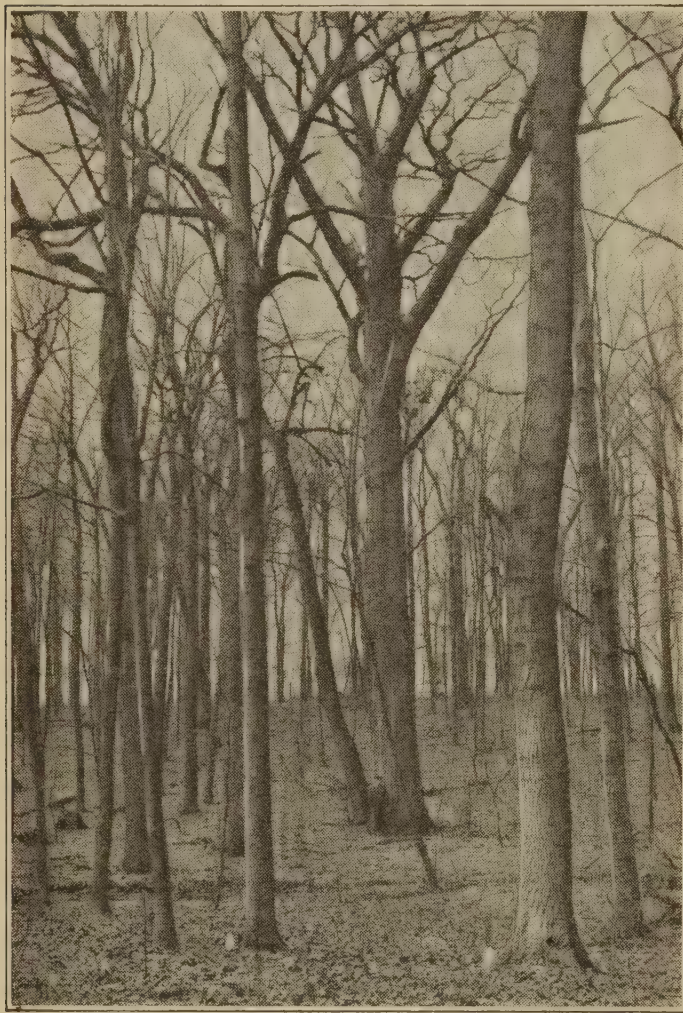


FIG. 496. Leafless condition of a deciduous forest in the northeastern part of the United States

portions which send up flowers and leaves before the appearance of the leaves on the trees and so make use of the bright light which reaches them before they are shaded by the foliage of the trees. The aërial parts of many of these plants disappear early in the season.

The changes in appearance which the forests undergo with the changing seasons are very striking. During the winter the trees are leafless and only a portion of the herbaceous vegetation retains its foliage. In the spring early flowering herbs carpet the ground and

flower profusely, while shrubs and trees burst into bloom. Most of the trees are wind-pollinated and have inconspicuous flowers, but some of them have conspicuous insect-pollinated flowers. At this time the great array of blossoms renders the forest an object of great beauty. In summer the foliage predominates and flowers are scarce. In autumn, before the trees



shed their foliage, the leaves of many of them change from green to brilliant shades of red, yellow, and brown, and again the forest is strikingly beautiful. As the brightly colored leaves fall the forest enters the period of winter rest.

**Coniferous forests.** Evergreen coniferous trees of the north temperate zone are adapted to withstand the desiccating effects of



FIG. 497. Summer condition of a deciduous forest in the northeastern part of the United States

winter by having xerophytic needlelike or scalelike leaves (Figs. 475, 479). The xerophytic structure of the leaves enables the trees to retain their foliage throughout the winter, the leaves of most species remaining on the trees for a number of years. The retention of the foliage throughout the year has the advantage that the leaves can carry on photosynthesis whenever conditions are favorable, while the same leaves can function for several seasons.

Undergrowth is usually less dense in a well-developed, temperate-zone coniferous forest than in a deciduous one. This



is due in part to the fact that in the coniferous forests there is no season during which the undergrowth is not shaded by the foliage of the trees, and in part to the fact that a carpet of slowly decaying, dry, resinous leaves hinders the establishment of seedlings.

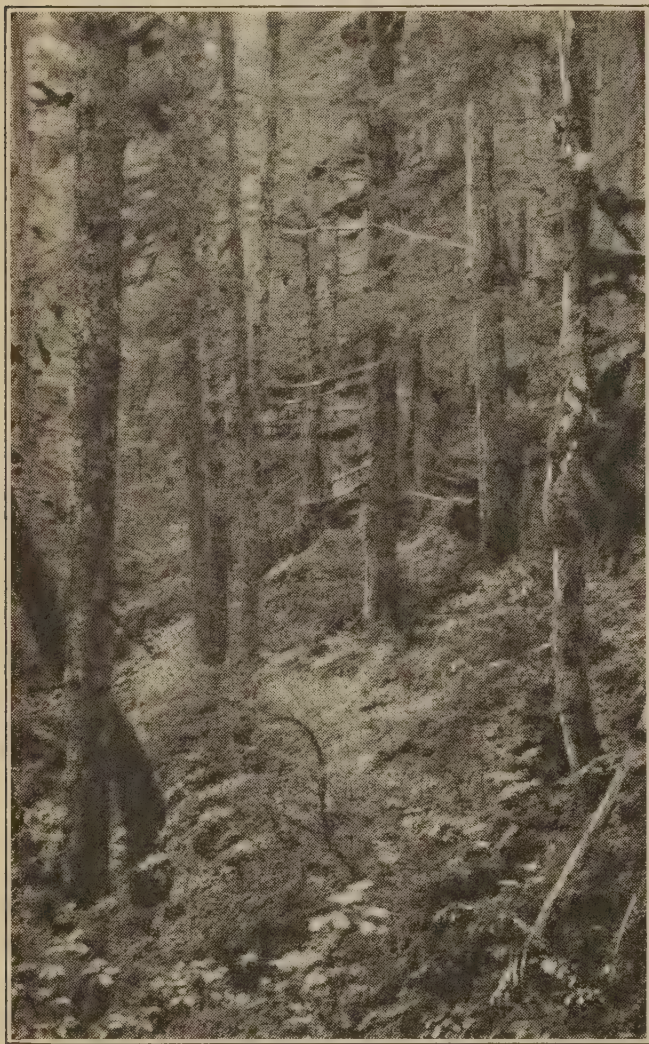


FIG. 498. Interior of coniferous forest, Taku Inlet, Alaska

The trees are *Picea sitchensis* and *Tsuga heterophylla*

Vast areas in the north temperate zone are covered by coniferous forests (Figs. 477, 495, 498). These are well developed in Europe, Siberia, and Canada, and in the northern, western, and southeastern portions of the United States. The northern boundary coincides everywhere with the limit of tree growth. The largest stands of timber in the world are found in the coniferous forests which appear on the western coast of the United States.

**Tundra.** From the standpoint of plant geography the boundary of the arctic region may be considered as the place where the last stunted trees disappear. This may be on either side of

the arctic circle. North of this limit, where ice does not cover the ground tundra dominates the arctic region. The growth is usually open and always dwarf, and mosses and lichens predominate. In favored situations there may be patches of meadows or dwarfed shrubs.





FIG. 499. *Pinus flexilis* at timber line, Longs Peak, Colorado

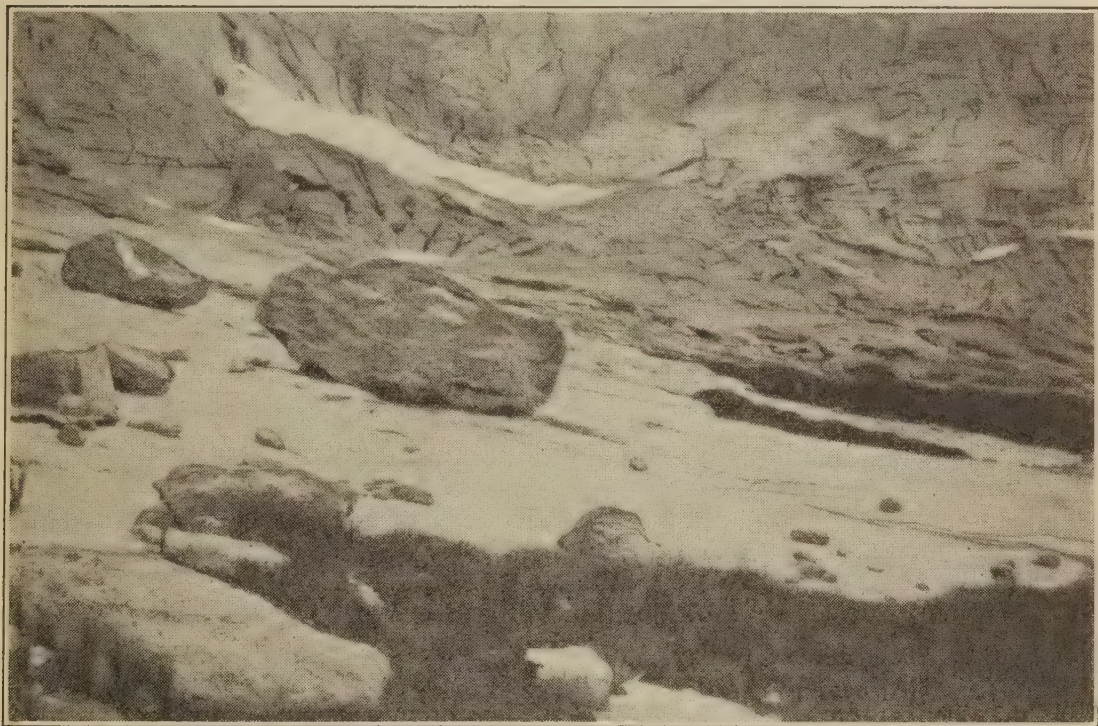


FIG. 500. Alpine meadow invading glaciated rock surface, Glacier Gorge, Longs Peak, Colorado



The growing season is very short, about two months, so that the spermatophytes rapidly pass through the stages from flowering to fruiting. One of the most striking characteristics of the tundra is the abundance and large size of the flowers as contrasted with the small, short stems.

**Mountain vegetation.** The vegetation at different altitudes on mountains is profoundly affected by the changes in climate

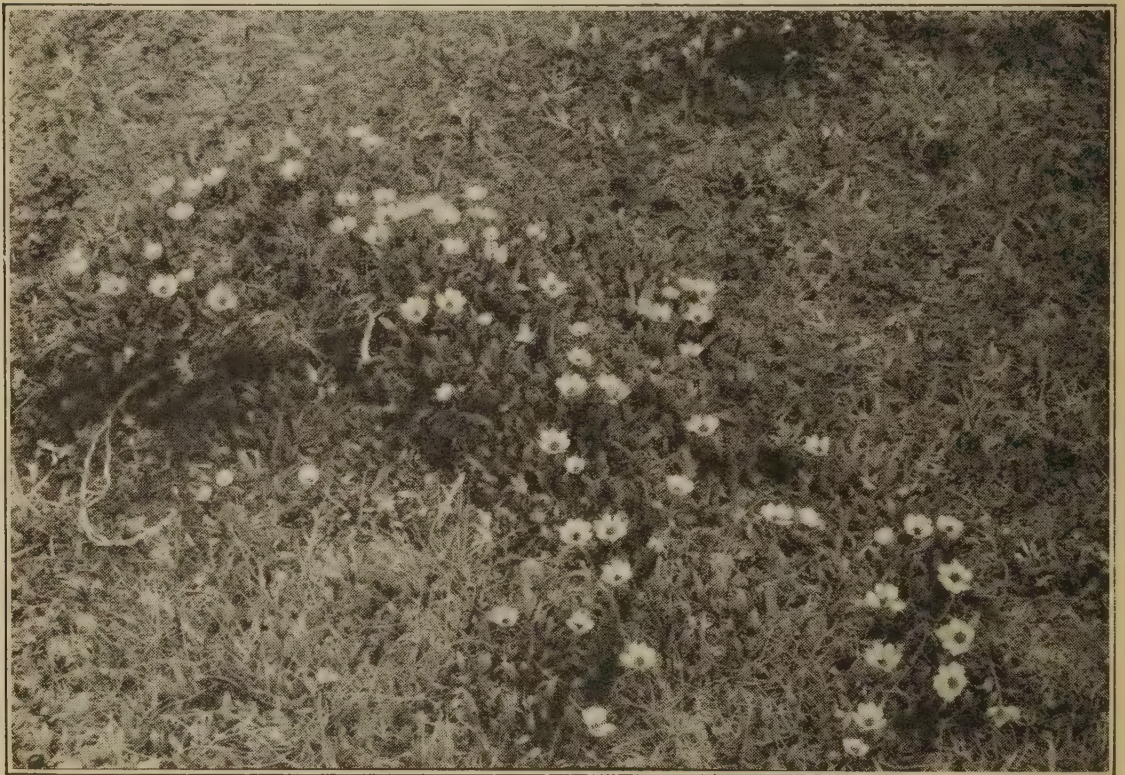


FIG. 501. Alpine meadow near Mount Robson, British Columbia

at different elevations. With rising altitudes the temperature steadily decreases until, if the mountain is sufficiently high, there is a perpetual cap of snow. Rainfall is usually heavier on the lower slopes of mountains than in the surrounding lowlands. This is due to the fact that as the warm air from the lowland is forced up the mountainside it cools, with the result that its water-holding capacity is lessened, and the consequent excess of water in the atmosphere forms clouds, which frequently give rise to rain. The amount of rainfall increases up to a certain altitude, and then decreases because, as the air continues



to lose water in the form of rain, it retains less and less moisture. The large rainfall at low and medium altitudes on mountains frequently results in a more luxuriant vegetation in these situations than in the neighboring and drier lowlands. The greater luxuriance of the vegetation at low and medium altitudes on mountains is particularly striking when the mountains



FIG. 502. Two-storied forest on Mount Maquiling, Philippine Islands, at an elevation of seven hundred and forty meters

rise from a dry or desert region. This is seen in Arizona, where the country around the mountains, and even the lower slopes of the mountains themselves, produce only desert vegetation, while at higher altitudes there occur rather luxuriant coniferous forests.

On mountains the height of the forests decreases with rising elevation. At low and medium altitudes a greater luxuriance sometimes results from increased rainfall, but with this exception the height of the forests decreases until, frequently, the



forest passes into elfin wood, which consists of stunted and twisted trees (Fig. 499). Above the elfin wood there is often an area of dwarf shrubs, which in turn gives way to alpine meadow (Figs. 500, 501). This consists of a short, xerophytic, matted vegetation of grasses or dicotyledonous herbs, or both. Where conditions are favorable this vegetation extends to the

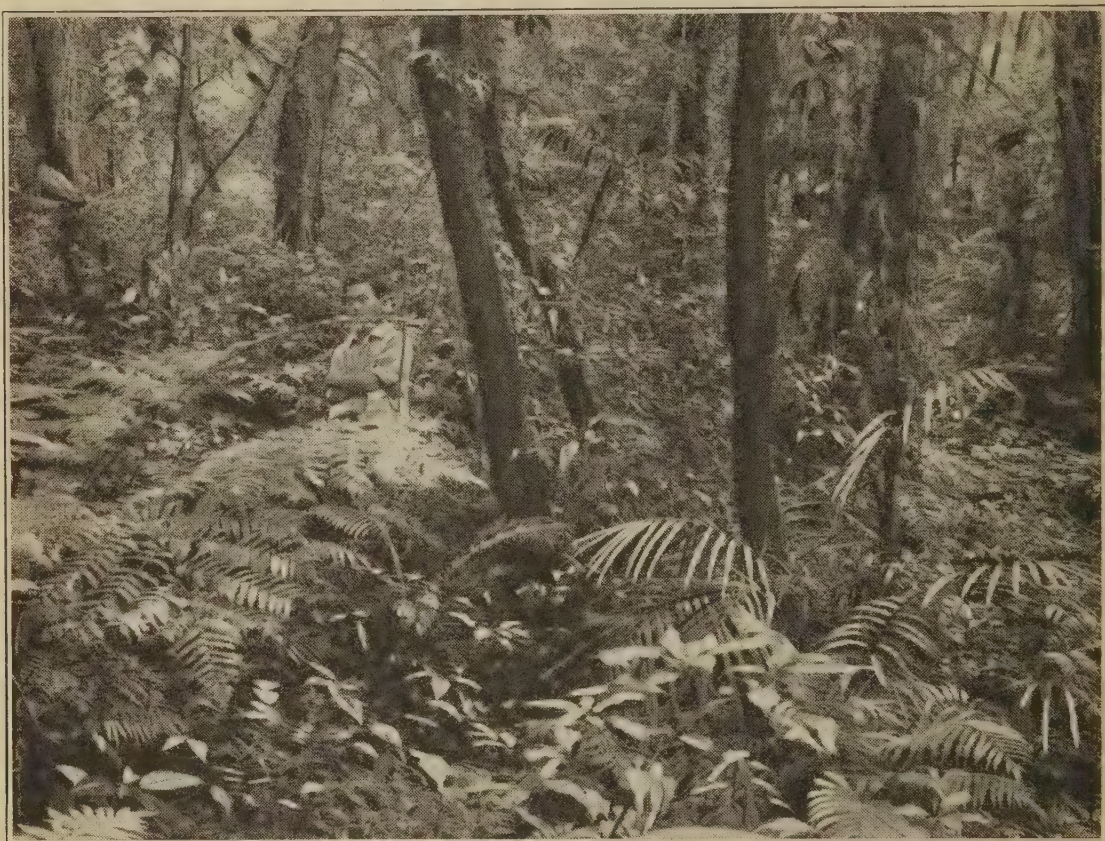


FIG. 503. Another two-storied forest on Mount Maquilang, Philippine Islands, at an elevation of seven hundred and forty meters

region of perpetual snow. As in the arctic tundra, the flowers of the alpine meadow are large in comparison with the dwarf plants (Fig. 501).

On moist tropical mountains the three-storied rain forests give way to a lower forest, which often consists of two stories, and which in many respects resembles the subtropical rain forest (Figs. 502, 503). It is less rich in species of trees than is the tropical rain forest and contains fewer woody vines and, usually, a smaller percentage of phanerogamic epiphytes, while epiphytic



mosses and liverworts are more numerous. In general, epiphytic vegetation is more luxuriant (Fig. 508) than in the three-storied rain forest. Above the two-storied forest there is an elfin wood



FIG. 504. Sclerophyllous forest in Australia in a region with an annual rainfall of thirty to forty inches

consisting of a single story of twisted trees (Figs. 505, 506). Usually the trunks and branches of the trees of the elfin wood (Figs. 506, 507), and sometimes those of the two-storied forest at higher altitudes, are densely covered with a thick mat of mosses and liverworts. The mosses and liverworts not only



cover the trunks and branches but also hang down in graceful festoons (Fig. 506). In the mosses and liverworts grow numerous ferns and a considerable number of flowering plants.

Flowers of epiphytes, vines, and trees are usually numerous in this mossy forest, and, owing to the low stature of the trees, are conspicuous. The small size of the trees and their twisted



FIG. 505. Lower part of twisted tree with many aërial roots in elfin mossy forest near summit of Mount Maquiling, Philippine Islands

form, the thick mantles and festoons of mosses and liverworts, and the numerous blossoms give the mossy forest a weird yet attractive appearance and make it one of the most striking types of vegetation found in the tropics.

**Monsoon forests.** In the tropics, regions with one or two pronounced dry seasons of several months' duration are much greater in extent than are those with a constantly humid climate. A seasonal climate is particularly characteristic of the interior of



continents. Where the rainfall is abundant during the wet season well-developed forests occur, but the vegetation is not so luxuriant as in the constantly moist regions. During the dry season the foliage is largely shed, the degree of defoliation depending on the severity of the season. Over large areas the loss of leaves is never uniform, as along watercourses trees retain their foliage throughout the year. Except when the dry season is extreme



FIG. 506. View in elfin mossy forest near summit of Mount Maquiling, Philippine Islands

Note how the trunks, branches, and aërial roots are covered with festoons of mosses

occasional evergreen trees occur. During the dry season the monsoon forests do not present as lifeless an aspect as do deciduous temperate forests in the cold season, as the dry season is preëminently the time of flowering.

Monsoon forests resemble the deciduous forests in temperate regions in being of lower stature than tropical rain forests. They are also similar to the temperate-zone deciduous forests, and



different from tropical rain forests, in that the trees have thick bark and annual rings of growth in the wood and lack buttressed roots.

**Xerophilous forests.** Dry tropical and subtropical regions which are not dry enough to produce deserts support either xerophilous forests (Figs. 241, 504) or grassland. The xerophilous forests may be either evergreen or deciduous. The trees are usually of



FIG. 507. Growth of mosses and a filmy fern on a trunk in elfin mossy forest near summit of Mount Maquiling, Philippine Islands

low stature as compared with rain or monsoon forests, but there are exceptions, the giant *Eucalyptus* forests of western Australia being pronounced xerophilous forests. The vegetation is more open than in rain forests or monsoon forests, and the leaves are much more xerophytic than in the latter types. The xerophilous forests often grade into bush land (Fig. 509), grassland, or desert.

**Grassland.** Grassland in tropical and subtropical regions usually takes the form of savanna, in which widely spaced trees occur with the grass (Fig. 510). In temperate regions grasslands are



usually without trees except along watercourses. In the United States the more moist grassland or prairie is excellent for raising grain, while the drier grassland or plain is good for grazing.

In many cases extensive grasslands are due to the interference of man rather than to natural conditions. In temperate regions meadows are frequently produced as a result of cultivation. In the Malay Archipelago large tracts of rank, waste grasslands are due to periodic fires which have followed the removal of the original forests. The fires destroy dicotyledonous plants but do not appreciably damage the underground rhizomes of the grasses. Similarly, fires are frequently responsible for the presence of grasslands in temperate areas.

**Deserts.** Areas which have a very slight rainfall and are covered by a scanty growth of scattered plants are known as deserts (Figs. 48, 511). The largest area stretches across Africa into southeastern Asia. In Africa it is called the Sahara Desert, and in Asia it is called the Arabian Desert. The next largest area includes most of central Asia. Large desert areas occur in central Australia and in Mexico and the western part of the United States, while small areas are found in southwestern Africa and South America.

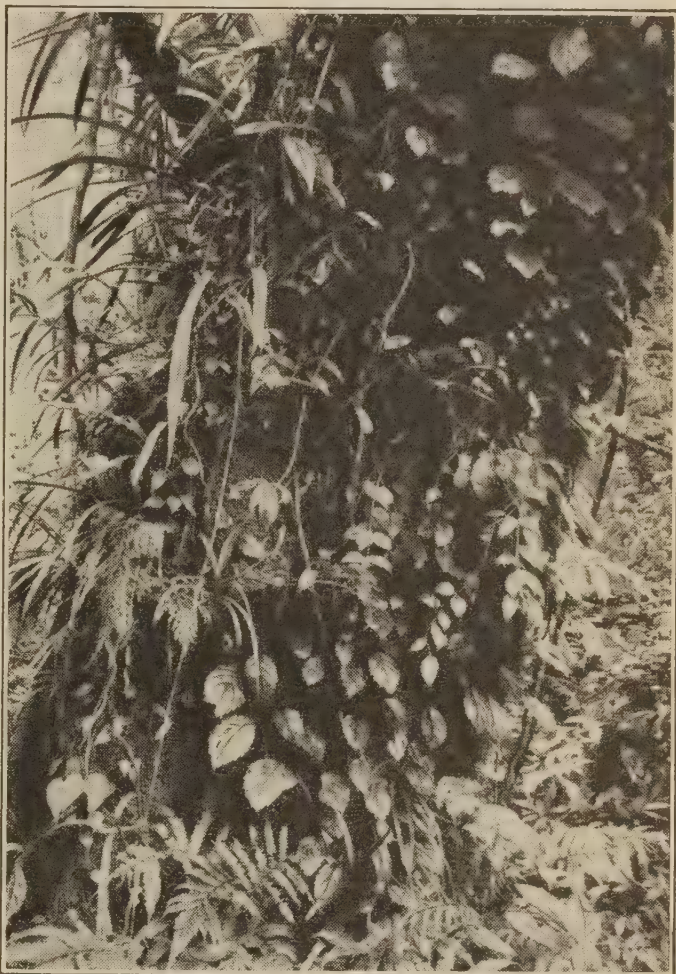


FIG. 508. Epiphytes on trunk near the upper limit of two-storied forest on Mount Maquilung, Philippine Islands



Deserts are characterized by an open growth of comparatively small plants many of which are thorny (Figs. 44, 512). Plants of desert regions are adapted in various ways to withstand adverse conditions. Some, particularly shrubs and shrubby trees, have long roots that reach down to subterranean water. The cacti have roots that spread near the surface of the soil. When the



FIG. 509. Bush land in Australia in a region with an annual rainfall of ten to thirty inches

soil is wet, considerable quantities of water are absorbed by the extensive root system and then stored in the enlarged stems. Deserts usually have a short rainy season when conditions are fairly favorable to vegetation and during which annuals spring up and pass through their whole development. Such annuals do not have a xerophytic structure. Other plants, with perennial underground portions, send up aërial shoots which disappear after the moist period. Some of the shrubs are leafless or have greatly reduced scale leaves; others have small, xerophytic,





FIG. 510. Savanna in a region in Australia with an annual rainfall of ten to thirty inches



FIG. 511. Desert region in Arizona



evergreen leaves; while still others are deciduous and have mesophytic leaves during the rainy period.

The appearance of deserts varies greatly according to the kinds of plants found in them. In many places the plants are largely shrubs (Fig. 513), while in other regions succulents are conspicuous (Figs. 512, 514). In parts of the American desert cacti



FIG. 512. Arizona desert with large *Opuntia*

predominate, while in parts of Africa, particularly in the south, there are numerous euphorbias with a general appearance similar to that of certain cacti.

The appearance of deserts also changes according to the seasons; during a dry period the vegetation is very scanty and has a gray or rather dirty green color, while in the rainy period the vegetation is much more luxuriant, owing to the presence of the annuals and of the mesophytic foliage on the deciduous perennials. At the same time flowers are frequently found to be very numerous.



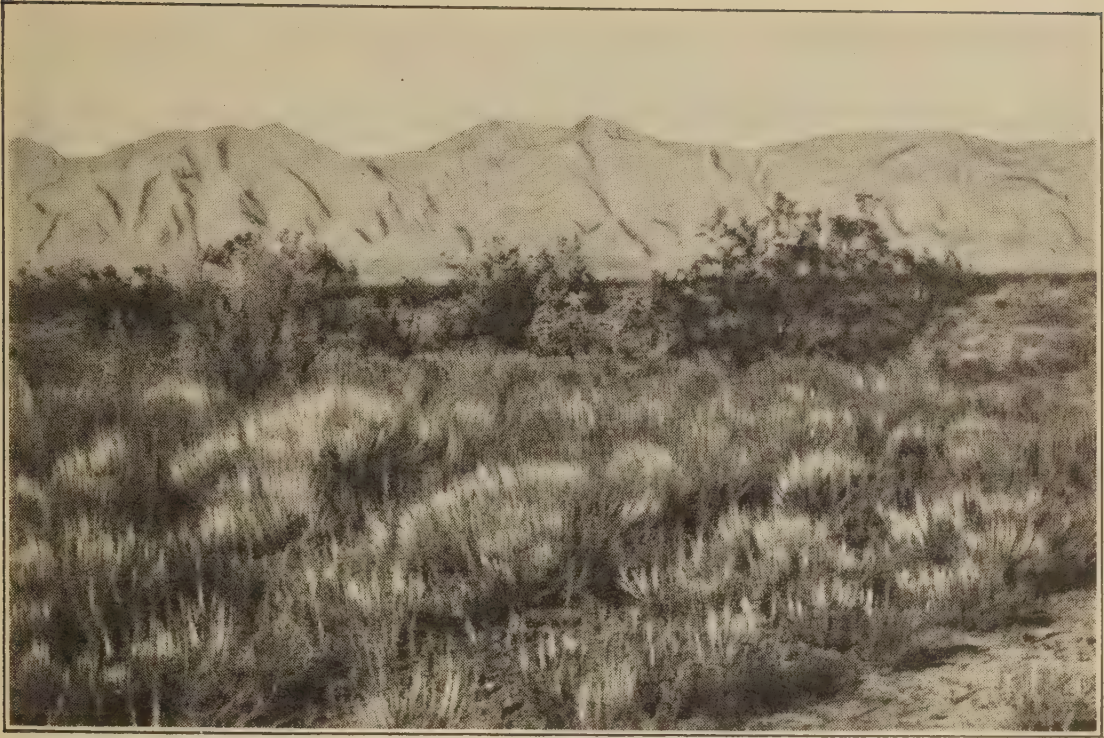


FIG. 513. Scene in Arizona desert

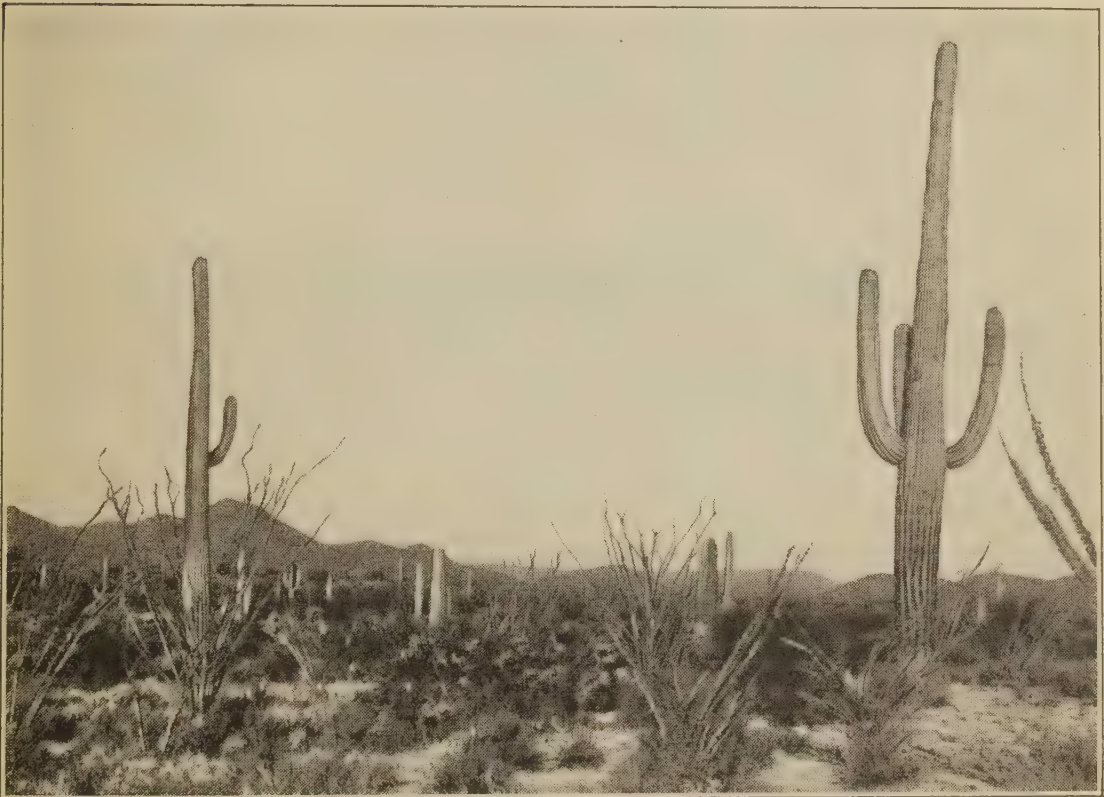


FIG. 514. Scene in Arizona desert  
Note the conspicuous giant cacti (*Carnegiea*)

**Marine vegetation.** In seas, floating microscopic algæ are numerous, and among them diatoms are prominent. These microscopic floating plants are the chief source of food for marine animals.

Macroscopic marine plants are either algæ or angiosperms, the algæ predominating. The angiosperms are grasslike plants but not true grasses, and grow rooted in sandy or muddy bottoms of calm, shallow bays. Macroscopic algæ are most abundant on rocky coasts; for the most part they are attached to the rocks, but they may be attached to other objects, such as shells or other algæ. Algæ occur not only below the level of low tide but between tide levels, and in cold temperate regions on rocky coasts the development of algæ between tide levels is very luxuriant. Macroscopic algæ range in size from small plants which are hardly visible to large ones many meters in length.

**Fresh-water vegetation.** In fresh water, as in salt water, microscopic floating algæ are very abundant, and among them diatoms are numerous. The macroscopic vegetation differs very greatly from that of salt water, as flowering plants predominate over the algæ, while the algæ are small as compared with those of salt water. The macroscopic plants may be divided into three general classes: submerged plants, rooted plants with floating leaves, and floating plants.

In general, plants which are entirely submerged grow in deeper water than do those with floating leaves. The conducting and strengthening tissues are very poorly developed in submerged plants. As they float in the water, they do not need strengthening tissue to the same extent that land plants do; and as they do not transpire, there is no necessity for any considerable development of water-conducting tissue. The leaves are thin and in many cases are finely divided, thus exposing large surfaces for the absorption of materials.

Plants with floating leaves have a conspicuous development of air spaces (Fig. 40). These serve as an aërating system for the diffusion of oxygen from the leaves to the roots. Moreover, the air spaces in the leaves are of assistance in enabling the leaves to float on the surface of the water.



Floating plants of cold temperate countries are all of small size, but they may be abundant enough to cover the surfaces of small ponds. In warmer regions floating plants reach larger size (Fig. 5), and the water hyacinth (Fig. 72) may obstruct navigation in sluggish streams. Floating plants are provided with well-developed air spaces (Fig. 71), which make the plants buoyant



FIG. 515. Lotus (*Nelumbium nelumbo*) projecting out of the water, and *Pistia stratiotes* floating on the water, in Laguna de Bay, Philippine Islands

and at the same time serve as passageways in which oxygen can diffuse to the roots. The roots hang down in the water and serve as a counterpoise which helps to keep the plant right side up.

**Swamp vegetation.** Around the edges of quiet bodies of fresh water, and in shallower water than that in which plants with floating leaves occur, there is often a conspicuous development of swamp composed largely of erect monocotyledonous plants with roots under water or in saturated soil and with shoots extending into the air (Fig. 515). Such plants contain conspicuous air



passages for the aëration of the roots. In other cases the shallow water is occupied by a growth of shrubs or trees. Salt-water swamps in temperate regions are occupied by a reedlike growth consisting largely of monocotyledonous plants. In the tropics mangrove-swamp forests are formed on mud flats, which are exposed at low tide and at high tide are covered by salt water.



FIG. 516. Interior of Philippine mangrove swamp at low tide

Note the aërating prop roots of *Rhizophora* and the erect aërating roots which project upward out of the mud

**Mangrove-swamp forests.** The term *mangrove-swamp forest* is applied to the type of forest occurring on tidal flats along tropical seacoasts (Figs. 197, 516). The conditions most favorable to their development are found in quiet bays into which flow large rivers whose lower reaches have little fall. The descending waters of the rivers are checked when they meet tidewater, and deposit their sediment in the form of broad flats or deltas near the mouths of the rivers. These flats are usually cut by a network of channels through which the advancing and receding water



of the sea moves. At extreme low tide the flats are exposed, and often even the larger channels are dry. On these mud flats the trees which form the mangrove vegetation find conditions favorable to their development; and as the seeds or seedlings of these species are distributed by water and can be transported for long distances without injury, the formation of flats and their seeding are almost simultaneous. When conditions are favorable,



FIG. 517. Aërating roots of *Sonneratia caseolaris* in Philippine mangrove swamp

new flats are formed beyond the old, and the forest advances year by year. The mangrove forests may contain trees more than a meter in diameter, and when fully stocked with mature timber compare favorably with the commercial forests of the land.

The mangrove forests are characterized by the presence of roots that show above the surface of the ground (Figs. 197, 517) and contain numerous air spaces that serve for the conduction of oxygen to the underground root system. In the genus *Rhizophora* these roots take the form of prop roots and serve both as props for the tree and for the aëration of the root system. In

some cases the aërating roots are slender structures which grow vertically out of the soil, while in still other cases they have the form of knees.

Another characteristic of a large proportion of mangrove-swamp trees is the germination of the seeds while still within the fruits. This feature is most strikingly shown in the family *Rhizophoraceae*, in which the seedling bursts through the fruit and hangs down as a long, slender structure while the fruit is still attached to the tree (Fig. 300). Finally the seedling drops from the fruit, sticks in the mud, and continues to grow (Fig. 301), or it may be transported by water and deposited in a situation that is favorable to growth.

**Succession and climax vegetation.** The large vegetational regions, such as rain forest, deciduous forest, deserts, and arctic tundra, are determined by climate, the principal factors being moisture and temperature. In all extensive regions there are, however, minor areas in which the vegetation is the result not of the general climatic complex but of purely local conditions such as the nature of the substratum or the interference of man. Vegetation that is in a stable condition and represents the highest type that the climate can support is climax vegetation. Before vegetation reaches a climax, or stable condition, it may pass through many successive stages that are influenced by the local environment. The giving way of one type to another is known as succession.

In a region in which tall forest is the climax type there may be a lake which results in the presence of several local types of vegetation. The vegetation in the deepest part of the lake in which there are rooted plants may consist entirely of submerged plants, and between these and the forest the following types of vegetation may occur in successively shallower water: plants with floating leaves, erect monocotyledons projecting out of the water, and a growth of shrubs. The level of the water in lakes does not remain constant; on the contrary, the depth of the water tends to become less and less. This is due to the fact that material is constantly being deposited in the lake and so



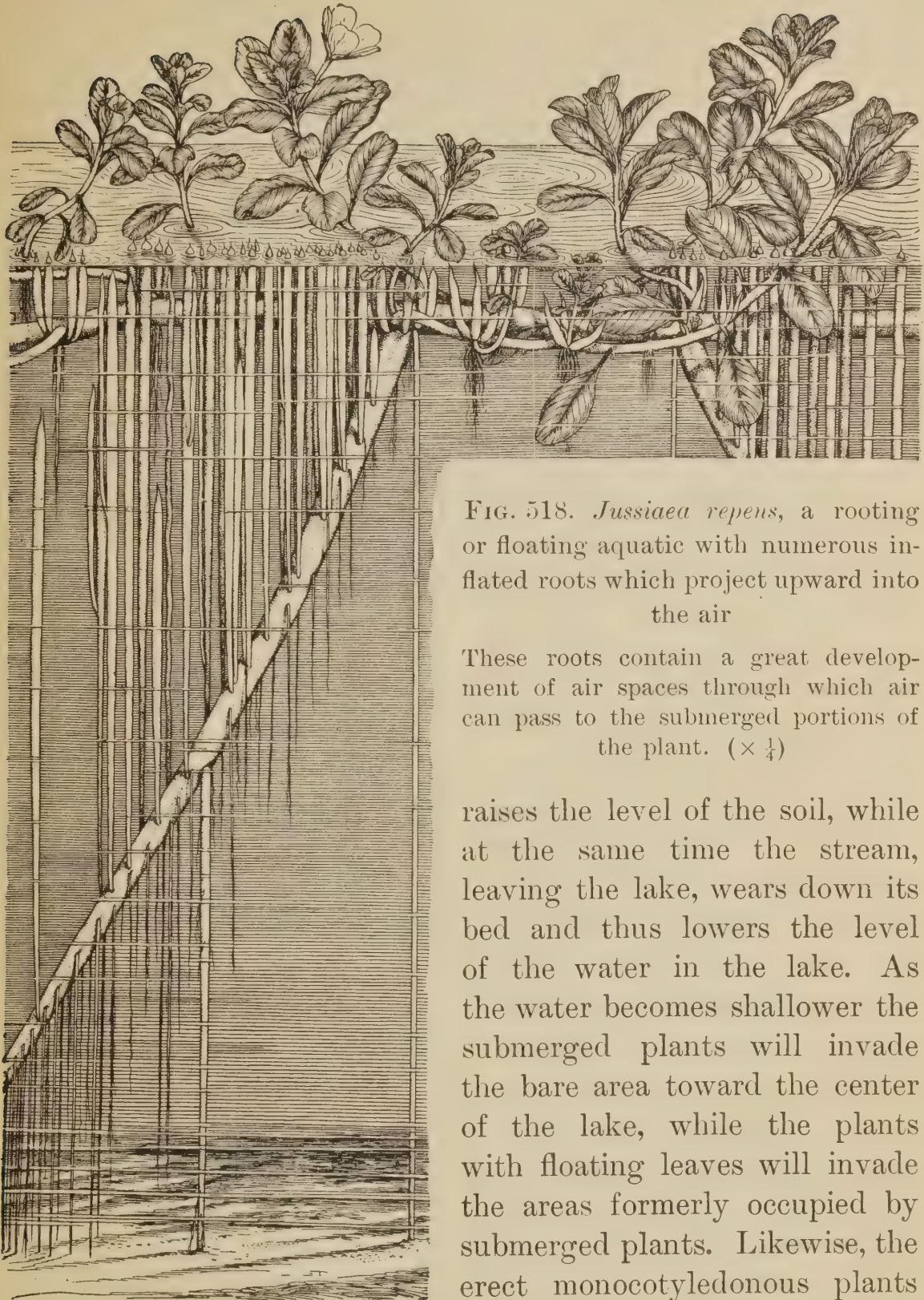


FIG. 518. *Jussiaea repens*, a rooting or floating aquatic with numerous inflated roots which project upward into the air

These roots contain a great development of air spaces through which air can pass to the submerged portions of the plant. ( $\times \frac{1}{4}$ )

raises the level of the soil, while at the same time the stream, leaving the lake, wears down its bed and thus lowers the level of the water in the lake. As the water becomes shallower the submerged plants will invade the bare area toward the center of the lake, while the plants with floating leaves will invade the areas formerly occupied by submerged plants. Likewise, the erect monocotyledonous plants will invade the areas previously

occupied by the plants with floating leaves, while the forests will invade the area which was swampy as the latter becomes dry.

Thus, there is a series of successions between the deeply submerged bare ground and the climax forest.

Rocks may support only a growth of lichens, but as the rock weathers and soil accumulates there is a series of invasions which ends with the climax forest.

On tropical coasts, mud flats are occupied by mangrove-swamp forest, but as the land is raised this is succeeded by the forest of the dry land and finally by the climax type of the region.

The types of plant successions are very varied, are due to a great variety of local conditions, and lead to many types of climax vegetation. A study of successions shows that vegetation is not static but dynamic, and that much of it is unstable and changing. Just as an individual passes through many stages of development before reaching maturity, so plant communities go through various stages, or successions, before the climax type is produced.



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